ON THE ORIGIN OF PLUMS: A STUDY OF SLOE, DAMSON, CHERRY PLUM, DOMESTIC PLUMS AND THEIR INTERMEDIATE FORMS

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ABSTRACT: In this paper the origin of plums is investigated through a study of intermediate forms of sloe and damson. Furthermore the role of cherry plum in connection with the evolution of plums is discussed, as well as the various opinions on the origin of husbanded and feral damson. There is general agreement that damson is the ancestor of our domestic plums. The cultivation of *Prunus insititia* since the Neolithic era, as well as the subsequent development and spread of domestic plums, have led to the emergence of several local varieties in both groups.

In order to be informed on the multitude of varieties and range of distribution, the author has collected great numbers of stones of damson varieties and related groups in various parts of Europe and Anatolia. Fruit stones of both damson and domestic plums are shown to have characteristic varietal differences. This study has revealed several morphologically intermediate forms of sloe and damson. The features of these forms indicate that they result from hybridization between sloe and damson, which implies a close relationship between the species.

The conclusions in this study are principally based on results from breeding tests of varieties of damson, sloe, cherry plums and the intermediates, performed during the years 1989-1997. The tests demonstrate that fruit stones of black-fruited damson varieties germinate readily and that the seedlings usually develop into normal shrubs or trees. By contrast, fruit stones obtained from damson specimens with yellow, green or red fruits show seed sterility or produce seedlings characterized by poor growth and viability. These features suggest hybridization and such specimens probably originate from crossings between damson and domestic plums. The characteristics found in the progeny of black-fruited damsons suggest that this group represents the original, botanical species.

Fruit stones of cherry plums, irrespective of the colour of the fruits, show high germination capacity while the growth of their seedlings is remarkably homogeneous and vigourous. The strikingly similar features of sloe and black-fruited damsons, the evidence of their close relationship derived from the hybrid forms and the absence of cherry plum features have led to the conclusion that (black-fruited) damson plums developed directly from forms of sloe. The extreme rareness of intermediates between damson and cherry plum and the striking differences in features between these species indicate that cherry plum did not play a role in the ancestry of the damson.

KEYWORDS: Botany, species, hybridization, intermediates, *Prunus*, sloe, damson, cherry plum, origin of domestic plums.

1. INTRODUCTION

The genus *Prunus* (Prunoidae subfamily, Rosaceae family) is generally subdivided into four subgenera: Prunophora (plums), Cerasus (cherries), Amygdalus (almond) and Padus (cherries with flowers in terminal racemes 'bird cherries'). The genus as a whole comprises 150-200 species, depending on the definition of species.

Within the Prunophora group sloe, cherry plum, damson and domestic plum constitute four closely related species. Sloe is a widely distributed natural species of the temperate parts of Europe and Asia. Cherry plums (*Prunus cerasifera* ssp. *divaricata*) occur wild in central and western Asia and probably also on the Balkans. Cultivated and naturalized cherry plums (*Prunus cerasifera* ssp. *cerasifera*) are widespread in Europe and Anatolia. Related to these species but geographically distant is the *Prunus salicina/triflora* group, cultivated in east Asia (China, Japan). Other wild plums in Eurasia include *Prunus brigantina*, an endemic plum with inedible fruits of the southwestern Alps (France, Italy) and two species related to cherry plum, which occur locally in the Mediterranean: *Prunus cocomilia* (Italy, Greece, Turkey) and *Prunus ursina* (Israel to southern Turkey). Russian researchers distinguish several species related to cherry plum in the Caucasus and central Asia (Komarov, 1941).

Damson (*Prunus insititia*) is considered the main progenitor of the large-fruited domestic plums. This species is thought to have originated in western Asia or southern Russia (e.g. Caucasus; Rybin, 1936) and subsequently to have spread over Europe and much of Asia by cultivation. Its simple reproduction from rootsuckers, plants which develop from roots at some distance from the primary tree, has certainly assisted its distribution in the past. Though the fruits of most *insititia* varieties are economically worthless, damsons are still much present in gardens, farm-yards, old orchards etc. Feral and possibly wild specimens occur

throughout Europe, North Africa and Anatolia. In France the species is common in hedgerows and waste places near villages. Rikli (1943-1948: p. 675) mentions *Prunus insititia* as a component of holm oak forest in the Tell Atlas, Algeria (altitude 1030-1150 m). Another more or less natural habitat of the plant includes open places in the jungle vegetation that has developed on former dunes along the southern coast of the Caspian Sea. All the same, Russian researchers state that in the former USSR no plums occur in a wild state (Komarov, 1941). It is not impossible that wild populations have disappeared through cross-breeding with cultivated specimens.

The foregoing means that the origin of damson plums is unclear. As a polyploid species, damson plums probably evolved from another species or from crossings between *Prunus* species. According to Rybin (1936) plums originate from crossings between sloe (*Prunus spinosa* L.) and cherry plums (*Prunus cerasifera* Ehrh.). Rybin performed experimental crossings between these species, which in one case produced a polyploid plum resembling the damson. Werneck (1961) assumes a great contribution of sloe in the parentage of some Austrian damson varieties, whereas in others (e.g. 'Weinkrieche') he found dominating features of cherry plum. His conclusions were based chiefly on the features of the fruit stones. Zohary & Hopf (1988) suggest that damson plums evolved directly from polyploid cherry plums; they reject the role of sloe in the ancestry of damson plums. On the other hand, Körber-Grohne (1996) attributes a significant role to sloe in the development of *Prunus insititia*.

Prunus fruit stones have morphologically distinct and genetically fixed features, which enables the identification of species and even most varieties of plums. This is of special advantage in *insititia* plums, since within this group other varietal differences are small (fruits 20-25 mm in size, usually round/oval, and blue to violet in colour).

Since 1989 the author has collected fruit stones of damson and related groups in various parts of Europe and Anatolia with the following objectives:

- To trace the unknown origin of damson and other plums;
- To expand the rather scanty knowledge of the number and geographical distribution of *insititia* varieties;
- To perform basic research in the form of breeding tests in order to compare seedlings of cherry plum, sloe and damson varieties with the maternal plants;
- To obtain reference material to facilitate identification of plum stones from archaeological assemblages.

2. STUDIES ON PLUMS

The earliest written information on fruit and fruit cultivation comes from Roman authors, e.g. Pliny and Columella (Roach, 1985). Illustrations of plum fruits are available from the beginning of book printing. Konrad Gesner illustrated the yellow-fruited 'Ziparte' of central Europe in *Historia Plantarum* (1516-1565), while the 'Gelbe Spilling', also a yellow-fruited *insititia* variety, is illustrated by J.Th. Tabernaemontanus (1588). Carolus Clusius (1583) published the earliest illustration of cherry plums (see also Körber-Grohne, 1996). Other old plum varieties, such as the English damsons, are illustrated by John Gerard (1597).

Studies with the aim to survey the number and value of plum varieties were carried out in the 18th and 19th centuries. One of the earliest inventories was drawn up by Jahn et al. (1850-1875). The described fruit varieties include almost 300 plum varieties, occurring in Germany alone. Dutch fruit varieties were listed by Berghuis (1868). In the first half of this century some specialized handbooks were published in the U.S. (Hedrick, 1911), in Britain (Taylor, 1949) and in Sweden (Dahl, 1943). Peyre (1945) describes the 'wild' and cultivated plums of France. Most of these works provide also illustrations and descriptions of the stones, which already indicates the significance the various authors attribute to this part of the fruit as a means of identification. In general, however, it is difficult to identify unfamiliar varieties from the illustrated stones alone (with the exception of Dahl, 1943).

The following publications highlight the importance of the fruit stones as identifying features. Röder (1940) found that the identification of plum varieties is greatly facilitated by the characteristics of the stones. His work includes several plates with fruit stones of (mostly) domestic plums. A table with indices of the fruit stones (and fruits) completes the study. Except for two varieties belonging to the var. *pomariorum*, Röder did not include the *insititia* plums in his research. In Austria, Werneck (1958; 1961) studied the latter group for two reasons. First, the rapid decrease of damsons and related groups at the time of research; and secondly, the proven hardiness of these nongrafted plums to winter conditions in Austria. In Austria domestic plums were killed off by several severe winters this century, so that selected varieties of *insititia* might be of great economic advantage.

Monographs on cherry plums are scarce; an informative study is that of Stika & Frank (1988) which deals with the variability and distribution of modern cherry plums (wild, economic and ornamental) including pictures of fruit stones.

A thorough study of ancient plum varieties in Germany and adjacent regions (Alsace, France and the north of Switzerland) has been published recently by Körber-Grohne (1996). The origin of the ancient, nongrafted varieties of plums and prunes, but also of cherry plums, large-fruited forms of sloe and hybrids between sloe and *Prunus insititia* is discussed in connection with their respective histories as revealed from archaeological assemblages.

It is impossible to enumerate here all the papers

which discuss and illustrate ancient plum stones. The following are mentioned (see also Körber-Grohne, 1996):

Prunus insititia	
Neolithic	Hopf, 1968
	Bertsch & Bertsch, 1947
Bronze Age	Jacquat, 1988
Roman Period	Baas, 1936; 1951
	Frank & Stika, 1988
	Maier, 1988
Middle Ages	Behre, 1978
	Gregor, 1995
	Knörzer, 1979; 1987
	Kroll, 1980
	Opravil, 1976; 1986a; 1986b
	Van Zeist, 1994
16th/17th century	Behre, 1978
	Van Zeist, 1988
Prunus cerasifera	
	Baas, 1936
	Kühn, 1995
	Stika & Frank, 1988
Prunus spinosa ssp. *macrocarpa*/*Prunus fruticans* (intermediates)	
	Kühn, 1995
	Opravil, 1976
	Van Zeist, 1988; 1994

3. SOME NOTES ON THE VALUE OF IDENTIFICATION CRITERIA IN PRUNUS

In general the identification of the discussed *Prunus* species does not present difficulties. Untypical cherry plums, e.g. specimens with shorter pedicels, may at first sight be confused with damson plums. Some local *Prunus* species in the eastern Mediterranean, such as *Prunus cocomilia* in Greece and Turkey and *Prunus ursina* in western Syria and Lebanon, may be confused with the related cherry plum because of their likeness in foliage and fruits.

The identification of groups at lower levels (subspecies, varieties) is usually more complicated. Such is the case with cherry plums: cultivated cherry plums (*Prunus cerasifera* ssp. *cerasifera*) and wild cherry plums (*Prunus cerasifera* ssp. *divaricata*) of western and central Anatolia differ only in minute detail. The subspecies *insititia* and subspecies *domestica* include such a wide range of forms with so many overlapping features that it is hardly possible to point out diagnostic features which clearly distinguish the two groups. Recently, Körber-Grohne (1996) has included the 'Roter Spilling' in the group of prunes (ssp. *oeconomica*) on the basis of the features of the fruits and fruit stones. Up till then, this variety had been regarded as an *insititia* plum. This indicates that the present division of the subspecies is not (or cannot be) settled on well-defined characteristics. A group that clearly shows features of ssp. *insititia* and ssp. *domestica* are the typical English damsons. By their properties, the small-fruited English damson varieties are rightly classified in the *insititia* group. The small-fruited forms, even though some varieties produce pyriform fruits, are no doubt identical to the continental *insititia* varieties (in terms of the size and shape of the fruits and fruit stones). Yet this country also produces varieties with large fruits and stones, e.g. Damson Merryweather and Bradley's King, which given the size of their fruits should be classified as *domestica* plums. Their fruits show some resemblance to prunes. In this case it is easier to name the variety than the subspecies under which it is classified. The presence of features of *insititia* as well as those of *domestica* in a group with such typical properties as damsons is in all probability the consequence of crossings between damsons and different groups of plums. According to Taylor (1949) varieties like Damson Merryweather probably resulted from such crossings, but the typical damson flavour and bitterness of the fruits were decisive for their classification under the *insititia* group.

The identification of varieties is often complicated, firstly because of the number of varieties, and secondly because the properties of these varieties are not always as constant as is often suggested. Properties such as fragrance and taste, the size of the fruits, their time of ripening, the degree to which the flesh clings to the stone and the presence of pubescence on young twigs are decisive factors used in the identification of *insititia* and *domestica* varieties (see for instance Hogg, 1884). But these features may vary considerably. Some of these properties depend greatly on the weather in the growing season and on early or late harvesting. Large yields generally produce smaller fruits (and stones). The degree of pubescence on one-year-old twigs depends greatly on habitat and possibly also on the nature of individuals. As an example we might consider 'St. Julien', a well-defined French variety. Pubescent and glabrous specimens of this variety have been collected in equal numbers in the Morvan region in central France.

A general feature in young *Prunus* specimens is spinescence. This is of special significance in cherry plums; in floristic works, the absence of spines is a discriminating identification mark of this species. Yet, of some 100 specimens raised from stones of various origin, almost all developed an abundance of immense spines in the third or fourth year of growth. This spinescence apparently decreases at an older age. Even old specimens of sloe often lose their characteristic spinescence.

Of all the identification marks, the features of the stones seem the most stable characteristics. Hedrick (1911) notes: "In describing the several hundred forms of plums for *The Plums of New York*, the stone has been quite as satisfactory if not the most satisfactory, of any of the organs of this plant for distinguishing the various

species and varieties". In fact the size of the fruit stones is the sole feature that may vary to some extent. Experience teaches us that the dimensions of the stones slightly decrease in fertile years, especially in the large-fruited commercial plums. The value of fruit stones as a means of identification is affirmed by various authors (Röder, 1940; Werneck, 1961). They state that the characteristics of the stones are constant, providing a decisive identification criterion, not only for the identification of the species, but particularly for determining varieties. This is true especially for the commercial plum varieties. In a 'blindfold' test, Röder (1940) could correctly identify 95 out of 100 varieties, just by examining the stones.

4. THE INTERMEDIATES

During the present investigation it became evident that quite a number of plants with *insititia*-type fruits have also features which are not typical of this species, but bear closer resemblance to sloe, e.g. in the properties of fruit stones, leaves, taste of fruits and/or length of pedicels. By contrast, intermediate forms of damson/domestic plum and cherry plum are rare and were found only in Italy, while no specimens intermediate to sloe and cherry plum were recorded. The morphology and the properties of fruit and fruit stones of these intermediate forms suggest a relationship between sloe and damson, which lends this group a particular interest in the discussion on the origin and historical development of plums.

Opinions differ on the taxonomical status of the intermediates. Reference works assume the intermediate specimens to be hybrids of sloe and damson plums, *Prunus* x *fruticans* (Tutin et al., 1968), or include them as large-fruited varieties of sloe (*Prunus spinosa* var. *macrocarpa*) (Hegi, 1906 ff.), *Prunus spinosa* ssp. *megalocarpa* and *Prunus spinosa* ssp. *ovoideoglobosa* (Werneck, 1961). Fournier (1977) includes the intermediate specimens in sloe as possible intra-specific hybrids. Apart from *Prunus fruticans*, Peyre (1945) distinguishes five large-fruited forms at species level. Körber-Grohne (1996) divides the intermediates into large-fruited forms of *Prunus spinosa* (var. *macrocarpa*) and hybrids of *Prunus spinosa* x *Prunus insititia*. This division is in some cases supported by chromosome research. Large-fruited specimens with 2n = 32:4x chromosomes belong to *Prunus spinosa*, which has the same number of chromosomes. Accordingly, specimens with 2n=40:5x chromosomes should originate from crossings between sloe and the hexaploid (2n=48:6x) damson (see also section 4).

As a consequence of their problematic definition, the nomenclature of the intermediates and botanical species is quite confusing. A summary of scientific and vernacular names is presented in table 1, while characteristics of the groups are described in section 5. For a clear understanding of the term 'intermediates': these plants display features of sloe as well as damson. Plants with fruits that are larger than sloe, but with other characteristics which fully match that species, are considered as intermediates. Similarly *insititia*-type plants with for instance wry fruits have also been included as intermediates.

In this study the term damson refers to the group of varieties with round or oval, small plums (*Prunus domestica* ssp. *insititia*) which occur throughout Europe. In fact, some of the true English *insititia* varieties from which the noun damson is taken differ slightly from the continental *insititia*s in their typical flavour and necked (pyriform) fruit shape. Well-known and widespread typical *insititia* varieties are the German 'Krieche' and the French 'St. Julien'. In everyday language the term 'bullace' is often applied to the entire group of *insititia* varieties. The author is of the opinion that the bullace, even though it is considered an (English) *insititia* variety, has so many features in common with sloe, that this name is unsuitable to cover all the *insititia* varieties. Other plums, often larger-fruited (Reine Claude, oval plums, round plums, prunes, etc.), have been categorized under 'domestic' or *domestica* plums (*Prunus domestica* ssp. *domestica*).

More than 30 intermediate specimens (see Appendix) discussed here demonstrate a seemingly random variation in size and shape of the leaves, length of the fruit stalks, tannin and sugar content of the fruits and growth habit, properties which display traits of sloe or damson plums. In practice, features of either sloe or damson predominate in most specimens. From the

Table 1. Scientific and principal vernacular names of species and intermediates.

Latin name	English	French	German	Dutch
Prunus x *fruticans*	Intermediate specimens	Prunellier à fruits gros	Wilde Kriech, Saukriech, Gartenschlehe, Kultur-schlehe (Werneck 1961)	Grootvruchtige sleedoorn
Prunus spinosa var. *macrocarpa*				
Prunus spinosa	Sloe, blackthorn	Prunellier, épine-noir	Schwarzdorn, Schlehe	Sleedoorn
Prunus insititia	Damson, bullace	Pruneolier, prune sauvage, crèque	Ziparte, Krieche, Haferpflaume	Kroosjes, kriekpruim, wichteries
Prunus cerasifera	Cherry plum	Prune-cerise	Kirschpflaume	Kerspruim

varying and interspecific features of the specimens, the author concludes that the specimens originate from crossings between sloe and damson.

4.1. Geographical distribution and habitats of intermediates

Written accounts indicate that intermediate specimens are distributed throughout central and western Europe (Domin, 1944; Peyre, 1945; Werneck, 1961; Woldring, 1993) and as far north as Småland in the south of Sweden (Weimarck, 1942). They are particularly common in France (Dordogne, Normandy, Morvan). Most of the discussed intermediates were collected in this country. According to Peyre (1945), particularly large numbers, comprising several types (according to Peyre: species), occur around the cities of Lyon and Bordeaux. Reports of extremely large-fruited (*spinosa*?) specimens occurring in Russia could not be verified. In an attempt to increase the range of grown fruit varieties, members of a Dutch pomological society (Noordelijke Pomologische Vereniging) requested Russian colleagues to send over fruit stones of such specimens. The sent samples contained a variety of *spinosa* stones, but hardly any exceeded 10 mm length, the minimum size for fruit stones of large-fruited specimens. The regions where intermediate specimens have been documented fall within the range of distribution of sloe and damson. Interestingly, intermediates seem to be absent in the southern European countries, although sloe and damson plums are widespread there. Davis (1956-1988) and Pignatti (1982) do not specifically mention these forms in their floras. Searches by the present author for intermediates in central and western Turkey, the Othris mountains in Greece and Tuscany in Italy, however, were indeed unsuccessful.

The discussed intermediates were mostly found in man-made habitats, such as hedgerows, along roadsides,

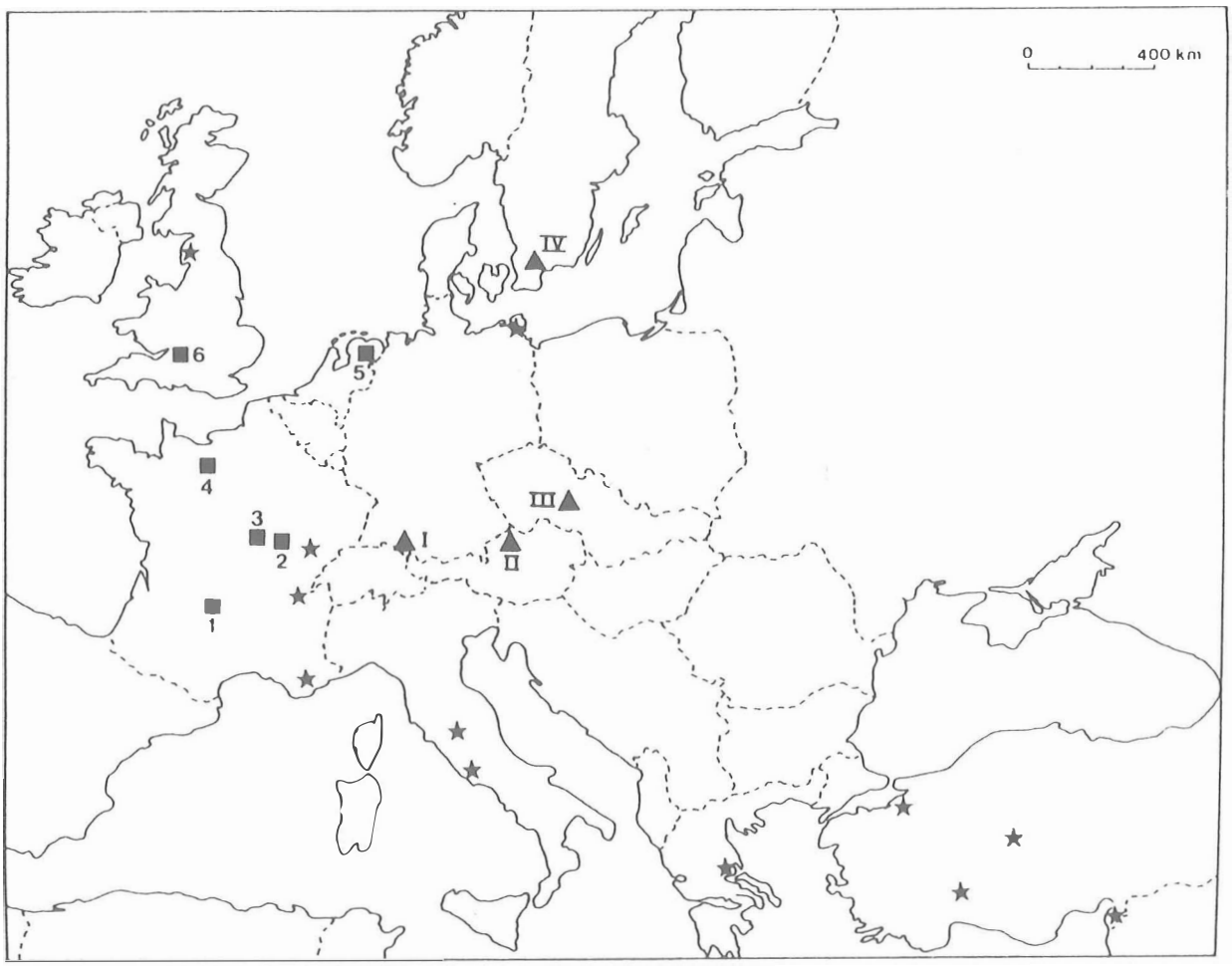

Fig. 1. Distribution of intermediates. The numbers indicate the occurrences of the discussed intermediates. 1. Dordogne, France, 10 types; 2. Côte d'Or, France, 5 types; 3. Morvan, France, 4 types; 4. Normandy, France, 5 types; 5. Northern Netherlands, 9 types; 6. Cotswold, UK, 2 types. The Roman numerals represent the records of intermediates/hybrids from literature: I. Bodensee (Körber-Grohne, 1996); II. Northern Austria (Werneck, 1958; 1961); Moravia (Kühn, 1995); IV. Southern Sweden (Weimarck, 1942). The asterisks indicate regions which lack intermediates.

edges of gardens, etc. They always grow near habitations or in the cultural landscape surrounding villages and hamlets. Seemingly spontaneous specimens appear to grow in the same habitats as sloe, such as hedgerows. Sometimes it was clear that the specimens had been planted. In France, cultivated specimens were encountered amidst different domestic fruit trees. Farmers in Normandy state that the wry fruits of these shrubs are consumed directly. Cultivated intermediates are also mentioned for Austria (Werneck, 1961). According to Werneck, the fruits are among other things used for the production of alcoholic beverages.

5. CHARACTERISTICS OF SLOE, DAMSON AND CHERRY PLUM

5.1. Sloe (*Prunus spinosa* L.)

Chromosome number usually (x=8) 2n=32 (4x), but also 2x (2n=16), 3x (2n=24), 5x (2n=40) and 6x (2n=48) (Watkins, 1976).
Shrubs or small trees, up to 3(5) m, spiny. Rootsuckers.
Leaves (ob)lanceolate, elliptic, (ob)ovate, 3-5 cm long.
Flowers 13-18 mm in diameter, borne singly.
Pedicels (3)5-10(15) mm long, diameter => 1 mm, pubescent or glabrous.
Fruits 10-15 mm in size, (sub)globose, ovoid, conoid, black(-violet), astringent taste, borne in rigid, non-drooping position. Mostly heavily bloomed. Ripe by end of August/September.
Fruit stones c. 7-10(12) mm long. The size separates *spinosa* stones fairly well from the other groups. Large *spinosa* stones overlap with the smallest in the other groups.
Tannin present. Citric acid absent (Komarov, 1941).

5.2. Damson (*Prunus domestica* ssp. *insititia*)

Chromosome number (x=8) 2n=48 (6x) (Watkins, 1976).
Shrubs or small trees attaining 4-8 m, spiny or unarmed. Rootsuckers.
Leaves elliptic, (ob)ovate or almost circular, 5-8(-10) cm long.
Flowers c. 25 mm in diameter, frequently in pairs, arising from one bud.
Pedicels (5)10-15(20) mm long, diameter >1 mm, pubescent or glabrous.
Fruits (15)20-25(30) mm in size, drooping, (sub)globose, ovoid or oval, usually bluish-black, but also yellow, red or green. Bloom mostly thin. Ripe in August-October.
Fruit stones (10)12-16(20) mm long. Ventral suture fairly complex, often broadened and with lateral grooves and ridges. Several types can be distinguished according to the varieties.
Tannin and citric acid present (Komarov, 1941).

5.3. Cherry plum (*Prunus cerasifera* Ehrh.)

Chromosome number usually (x=8) 2n=16 (2x), but also 3x (2n=24), 4x (2n=32), 6x (2n=48) (Watkins, 1976).
Many-stemmed shrubs or trees, up to 8 m. Rootsuckers absent.
Leaves (mostly) serrate, (ob)ovate, elliptic, oval.
Shoots thin, glabrous and smooth, usually unarmed.
Flowers borne singly. Blossoming (in northwestern Europe) c. 2-3 weeks before the other groups.
Pedicels (10)15-22(25) mm long, diameter =>1 mm, often between 0.6 and 0.9 mm, green orreddish, glabrous.
Fruits red or yellow, more rarely black-violet, green, orange, brownish; drooping, ripening early, bloom thin if present: June (Mediterranean), July, August.
Fruit stones 10-22(27) mm long. Ventral suture sharp-angled. Lateral grooves shallow, indefinite and mostly smooth lateral faces. In some Mediterranean cherry plums elevated lateral ridges are found.
Citric acid present. Tannin absent (Komarov, 1941).

5.4. Characteristics of the intermediates and comparison with sloe, damson and cherry plum

The following features describe the discussed intermediates: shrub or small tree, spiny or unarmed. A common feature of intermediates, sloe and damson plums is the abundant development of rootsuckers. A seemingly random variation exists in the size and shape of the leaves, which either resemble those of sloe or damson plums. Flowers, single or in pairs, 18-25 mm in diameter (measurements provided from specimens in the Netherlands), and frequently equalling those of damson in size. Intermediates blossom at the same time as sloe and damson (in the Netherlands, around mid-April). The fruits, c. 15-25 mm in size, are mostly globose or oval, occasionally subglobose or ovoid. This suggests a considerable variation, but broadly speaking one could say that the fruits of the intermediates are round or oval, c. 20 mm in size, purple to almost black and mostly with thick bloom (like the fruits of sloe). The features of the fruits largely match those of damson and differ from those of sloe only in the larger dimensions. Ripe fruits often tend to droop, like those of damson plums. The taste is variable: sweet, sour or astringent, depending on the tannin and sugar content of the fruits. The chromosome number of the intermediates is discussed in 6.2.

The dimensions of the fruit stones of the intermediates (length c. 10-15 mm) generally exceed those of sloe. In size, stones of the intermediates largely overlap with damson and cherry plum stones. A frequent feature of intermediates are the irregular indentations on the dorsal side of the stones (fig. 1). The stones of intermediates range in characteristics between true *spinosa* type stones

Table 2. Summary of the dimensions (in mm) of some morphological features of the discussed intermediates and the botanical species; * derived from Dutch specimens only.

	Diameter of flowers*	Length of fruits	Length of fruit stones	Length of pedicels	Diameter of pedicels
Intermediates	18-25	15-25(28)	10-15(18)	4-12(18)	(0.8)0.9-1.5(1.8)
Sloe	(13)15(20)	10-15(17)	≤10(12)	(2)4-12(15)	(0.7)0.9-1.5(1.9)
Damson	(18)20-25(28)	(17)20-25(30)	10-18(20)	10-15	≥1
Cherry plum	(20)25-(28)	20-30(35)	≥10	(10)15-20(25)	(0.4)0.5-0.9(1.1)

and *insititia* type. In the majority of the stones *spinosa* features dominate e.g. heavy sculpture, domed lateral sides, rounded outline (e.g. plate I, appendix), whereas in other types *insititia* features predominate, e.g. elongated, relatively flat stones, often with more or less pronounced s-shape (e.g. plate V, appendix). Stones of the last type resemble those of damsons so much that in many cases other features, such as *spinosa*-type leaves or wry fruits, must be used to distinguish the specimens from true damsons. Nevertheless, with some specimens it remained unclear whether one was dealing with an intermediate or with a true damson. It should be noted here that some *insititia* varieties exist such as the Dutch *kroosjes*, of which sculpture and shape of the stones are basically identical with the general characteristics of *spinosa* stones (see also Kroll, 1980).

The properties of the intermediates described here indicate a close relationship with sloe and damson. The intermediates lack the typical features of cherry plums (glabrous, thin and long pedicels, shape and serration of the leaves, glabrous twigs and the lack of rootsuckers). These differences indeed suggest that cherry plums are not involved in the ancestry of the West-European intermediates.

This does not imply that crossings between sloe and cherry plums do not occur. Sterile triploid hybrids (2n=24; 3x) between those species seem to be common in the Caucasus (Rybin, 1936). Zohary & Hopf (1988) note that "*domestica* and *insititia* plums apparently intercross and intergrade with *cerasifera-divaricata* forms". The present author found three almost identical trees which showed a true mixture of both aggregates near Tuoro, north of the Lago di Trasimeno in central Italy (*cerasifera* features: early flowering, fruits, foliage; *insititia/domestica* features: fruit stones, pubescent twigs, one specimen with rootsuckers). The intermediate traits suggest that these specimens originate from crossings between *cerasifera* and *insititia/domestica* plums.

6. GENETICS AND THE POSSIBLE ORIGIN OF INTERMEDIATE SPECIMENS

Theoretically, four genetic processes might lead to forms that are morphologically intermediate to sloe and damson.

6.1. Autopolyploidy

In this process, one, several or all chromosomes of a genome are duplicated or multiplicated. Morphologically, autopolyploidy may take shape in the enlargement of some or all parts of the plant. Thus, larger fruits might result from such a process in sloe. Retarded growth, decreased amount of branching, longer time of flowering, later flowering and reduction of seed fertility are features which may distinguish autopolyploids from the original species. During the study, no differences of this nature between sloe and the intermediates were noticed. In addition, sloe is a polyploid (4x), while the occurrence of autopolyploidy seems to be a regular feature in diploids only (Stebbins, 1960). The presence of *insititia* features in most intermediates also suggests a different origin. Two identical large-fruited specimens from Sainte Marie-en-Anglais in Normandy (see Appendix) might represent autopolyploids of sloe. These specimens differ from the common sloe only in the strongly enlarged fruits and stones.

6.2. Hybridization

Spontaneous and experimentally obtained interspecific (and even intergeneric) hybrids are fairly common in the Prunophora. Some examples:

- Crossings between sloe and cherry plum have been experimentally achieved by Rybin (1936). He also states that hybrids of these species are common in the Caucasus;
- According to Hegi (1906 ff.), mirabelle (*Prunus insititia* var. *cerea*) arose from crossings between cultivated plums and cherry plum;
- A peculiar specimen collected by the author in the mountains south of Isparta, southwestern Turkey, was

identified by Professor Browicz (Poznan, Poland) as a hybrid between *Amygdalus communis* and a *Prunus* species (probably nearby-growing cherry plum);

- Numerous experimentally obtained hybrids have resulted from efforts to improve the quality of fruits, adaptation of trees to environment and resistance to diseases, especially in America, e.g. crossings of Japanese plums (*Prunus triflora)* x native American species (Hedrick, 1911).

The morphological features suggest that the intermediate specimens result from crossings between sloe and damson. Chromosome research on two specimens has confirmed hybridization between these species. Analysis of an intermediate specimen near Lake Constance in southern Germany showed a chromosome number of 2n=40 (5x), intermediate to that of sloe and damson (Körber-Grohne, 1996). The same chromosome number was found by Weimarck (1942) in hybrids between sloe and the so-called 'terson' or 'tersen', an *insititia* variety of southern Sweden.

6.3. Sexual reproduction

Downing, a nurseryman from New York (1896), notes: "When reared from seeds, our fruit trees always show the tendency to return to a wilder form". This trait hints that our fruit trees are domesticates which would not occur in nature. Generally, seedlings of damson have a more spiny habitus than the parent plants. Notwithstanding their 'wild' appearance, seedlings of damson plums retain the diagnostic features of the species, above all in their fruit stones. Evidence for this statement may be found in the 'St. Julien', a variety that in the last centuries has been the chief rootstock for grafting plums in France. Until recently, its reproduction occurred from seed. In spite of this long tradition the fruit stones have remained quite uniform in their appearance. Another example is represented by the German 'Krieche', which according to Körber-Grohne (1996) has not changed significantly. Modern fruit stones of the 'Krieche' are identical to those found in excavations in southern Germany and in Swiss lake-dwelling settlements.

However, the mix of *spinosa* and *insititia* features in most intermediates make it unlikely that we are dealing here with 'reverting' *insititia* specimens, since the emergence of features of a different species (sloe) in those plants would be impossible. The origin of the intermediates must therefore be a different one. The possible origin of some questionable *insititia* specimens is discussed in section 8.1.

6.4. Apomixis

Specific pollinating processes have contributed to a great variability and the establishment of several micro-species in members of the Rose family (Rosaceae). Fairly common is apomixis, a reproductive process in which fertilization takes place without transfer of the genetic material of the pollinator. The progeny or the F_1 population is therefore identical to the maternal plant. Reproduction by apomixis is usual in e.g. blackberries (*Rubus fruticosus* s.l.), Lady's mantle (*Alchemilla vulgaris* agg.) and cinquefoil or tormentil (*Potentilla* species).

Chance cross-fertilizations in apomictic species produce F_1 plants which are morphologically intermediate to the parent plants. Continued apomictic reproduction (F_2) of the intermediate plants leads to a new micro-species. Although these F_2 plants differ only slightly from the parent species, authorities rank such new forms at species level, e.g. in *Rubus fruticosus* (Hegi, 1906 ff.).

A comparable process occurs in the usually self-pollinating dog rose and its siblings (*Rosa canina* complex). Again cross-pollination between related (sub)species occasionally alternates with the usual process of self-pollination. Because of its dominating genetic influence, the progeny of cross-breeding species in the *Rosa canina* complex differs only slightly from the maternal plant. Continued reproduction of the progeny by means of self-pollination leads to the formation of a new subspecies or micro-species.

The great number of varieties and strains in sloe and damson and the minor differences between them might suggest similar processes in these species. Such is not the case. It is stated in the literature that cross- and self-pollination are common (Taylor, 1949), whereas reproduction by apomixis is nowhere considered a serious possibility.

7. SOME RESULTS OF BREEDING EXPERIMENTS

A great number of seedlings have been grown from several varieties of the discussed species and intermediate forms, in order to provide insight into the reproductive capacities of varieties, the characteristics of the offspring, and possible differences in fruits and fruit stones, viability, rate of growth and growth habit among seedlings and between the seedlings and the mother plants. The experiments were undertaken also to test a statement in the literature (e.g. Werneck, 1961: p. 25) to the effect that the fruit stones of seedlings of *Prunus* varieties are morphologically identical to those of the maternal plant. Also segregating progeny would be evidence of hybridization between species and might therefore provide significant information on the origin of the intermediates.

Stones for sowing were selected from reference samples. It was decided to sow limited numbers of stones from a range of varieties. Because of their

complex nature, priority was given to the sowing of intermediates, but the experiments also included several varieties of cherry plum, damson and some strains of sloe. The tests started in 1989 and notes were made on germination capacity, viability and growth. Part of the seedlings of the starting years have blossomed and, notably the cherry plums; also set fruit. In cherry plums, first fruits appeared in the fourth or fifth year of growth, but in the same timespan fruiting succeeded also in some specimens of sloe. In general, fruiting occurs in the second or third year of flowering. No fruiting has yet been achieved in damsons and intermediates.

A conspicuous feature revealed by the breeding tests is the variation in (rate of) growth among seedlings from the same plant. This variation has been noted chiefly in *insititia* progeny, but also in seedlings of some *spinosa* strains. This heterogeneous growth suggests heterozygosity and is defined in genetics as the effect of the fusion of genomes of genetically different genotypes (cross-breeding plants). Each plant has thousands of genetic factors, genes which determine the individual characteristics. Cross-fertilization therefore gives an almost infinite number of potential recombinations (the seedlings). By contrast, self-fertilizing plants produce homozygous progeny, which only shows the genetic variation of the parent plant. The appearance of heterozygous progeny is therefore evidence of cross-breeding.

7.1. Sloe

Average germinative capacity: c. 60-80% (Grisez, 1974: c. 90%). Seedlings of the same origin show moderate to fairly vigorous and uniform growth, but the progeny of some strains shows more variation in growth and/or growth habit. The height of the different breeds varies between 20-30 to 60-80 cm by the end of the first growing season. Variation in growth between breeds is thus more pronounced in this species than in cherry plums (see below). This apparently is due to the wide range of forms (low to tall shrubs, small trees) existing in sloe.

In sloe the first flowers appear 4-5 years after germination.

7.2. Cherry plum

Germination rate: c. 70-80% (Grisez, 1974: 58%). One-year-old seedlings measure 50-100 cm or more and show uniform growth. Many specimens flower and fruit after 4-5 years. The first results show that fruit stones of the seedlings conform fairly well to the maternal plant. This does not hold for the colour and shape of the fruits, which either differ from or are identical to the maternal plant. A yellow-fruited specimen from Sölöz (Iznik Gölü, Turkey) yielded one red and several yellow-fruited F_1 specimens. Seedlings from a black-fruited specimen in the Jura (France) have so far produced fruits in several colours: red, brown-orange and bright yellow, but none having the black fruits of the parent. Shape and size of the fruits also differ from those of the parent. The fruit stones are copies of those which were sown.

7.3. Damson plum

Germination rate: 0-70% (Grisez, 1974: 89%). A most prominent feature observed in the offspring of *insititia* varieties is the variability in growth, not only between varieties and strains, but also among seedlings of the same plant. The dissimilar development of the seedlings is most pronounced at the end of the first growing season. One-year-old seedlings of the same origin may vary in height between a few centimetres and one metre. The smallest specimens often show little viability and part of them perish in the winter season. The variable growth is attributed to a heterozygous origin of the offspring.

Interesting contrasts are found between dark blue-purple-fruited varieties and those with differently coloured fruits (green, yellow, red or two-coloured), especially with regard to the germinative capacity of the stones and growth capacities of the seedlings. Usually, the stones of the dark-fruited category germinate readily. By contrast, stones of varieties with light-coloured fruits show failing or poor germination while the seedlings show poor growth. The straggling growth is frequently accompanied by characteristic growth deficiencies, such as multifold branching, easily breaking twigs and insufficient development of roots. Two- to four-year-old specimens died back almost to ground surface in the cold winter of 1995/1996. Such characteristics are very likely to be a consequence of hybridization.

The following cases suggest that hybridization has resulted in seed sterility. As reference material, fruit stones were collected from c. 150 *insititia* plants, the identification of which was based particularly on the characteristics of the fruit stones. Only two of these samples were collected from specimens with two-coloured fruits. One large tree with purple-and-yellow fruits was found in Groningen, the Netherlands, the second specimen grew in Les Piards, a village in the Jura, eastern France. Both specimens produce fruits which are somewhat larger than the average damson fruits. Other peculiarities are the king-size leaves (up to 11 cm) of the Groningen specimen (*insititia* leaves usually measure 5-7 cm) and the many-stemmed, dwarfish habitus of the Jura specimen. Stones from both specimens were sown. Fifty stones of the Groningen specimen, sown in two successive seasons, failed to germinate. Later examination of fresh fruit stones from

this tree confirmed the absence of viable endosperm. Twenty stones of the blue-and-yellow-fruited Jura specimen yielded five very similar and seemingly healthy seedlings, but the height of c. 50 cm which these specimens attained in six growing seasons illustrates an unusual stunted growth (a height of 2 or 3 m in the same period is common in most dark-fruited varieties).

Considering the characteristics, these specimens might be crossings between dark-fruited *insititia* specimens and a category of plums with larger and light-coloured fruits such as greengages (Reine Claude), a group that includes several varieties with large and green to yellow fruits.

According to Stebbins (1960) failing germination and inhibited growth are pronounced features of hybridization between related species and between groups (populations, varieties) within a species. They might result from the lack of homology between chromosomes of the parents of the hybrid. Judging by the list of examples cited by Stebbins, this is a widespread phenomenon in the plant kingdom.

7.4. Intermediates

Germination rate: 20 to 80%. The progeny of many intermediate types shows vigorous growth, and seedlings of the same parent are usually remarkably uniform in morphology. So far, segregating features, which characterize hybrid offspring, have only been observed in the progeny of an intermediate form near Gieten, the Netherlands (GIE-90-2). Two specimens (out of 30) have leaves resembling those of damson plums. Several seedlings show slightly smaller flowers than the hybrid, suggesting the involvement of sloe in the parentage of this specimen. Variable progeny, pointing to heterozygosity, is not common in this group. The progeny of some intermediate types is slightly heterozygous, but less markedly than in seedlings of damson plums.

Seedlings first blossomed at the age of 5-6 years. Fruiting has not yet been observed.

8. DISCUSSION

8.1. The origin of the intermediate specimens

As has been explained in the preceding section, the characteristics of the intermediate specimens resemble those of sloe and damson. The properties of the fruits, the presence of rootsuckers, flowering time, the frequency of pubescent twigs, length of pedicels, etc. contrast sharply with the characteristics of cherry plums. This suggests that sloe and damson are involved in the parentage of the interspecific forms. The processes that theoretically might have produced them have been considered in section 6 and will be briefly reviewed here.

Features of autopolyploidy, as pointed out by Stebbins (1960) are mostly lacking in the intermediates. Besides the absence of these features, the specimens were all found at sites in man-made habitats, such as hedgerows, orchards and waste places near human habitation. By contrast, intermediates are conspicuously lacking in natural and isolated plant communities with sloe. This also argues against an autopolyploid origin from sloe, for in that case large-fruited specimens would also arise in places where only sloe occurs. Features of damson in most intermediates also make autopolyploidy unlikely.

The presence of traits of sloe in most intermediates also seems to exclude the possibility of 'regressive' *insititia* seedlings, but some questionable specimens with dominating *insititia* features may actually be seedlings of damson plums. Apart from these particular cases, the interspecific and variable morphological features and other traits suggest that the specimens originate from crossings between sloe and damson.

The variable morphology of the hybrids/intermediates contrasts strongly with the mostly homogeneous progeny produced by individual plants. The plants grown from fruit stones of intermediates in many cases resemble the parent. This feature of the progeny conflicts with Mendelian rules of hybridization, which say that F_1 hybrids of the same parent plants are quite uniform, but that F_2 progeny segregates into types which partly resemble the parent plants. The value of progeny tests in providing evidence of hybridization is clearly demonstrated by Stebbins (1960: p. 25) and others. They found evidence for segregation of the progeny of hybrids of two species or other genetically distant groups, segregations which include types resembling the hybrid and types resembling the parents of the hybrid. Why the progeny of the hybrids does not segregate can only be guessed at. The homogeneous growth of the progeny suggests homozygosity and would indicate self-fertilizing hybrids. In that case the progeny is identical and varies only within the genetic limits of the parent plant. Self-fertilization is, however, unlikely to be a much more pronounced feature of hybrids than it is in the parents. If that were the case it would be natural for larger numbers of identical intermediates to occur in regions where intermediates are common.

It seems almost impossible to regard the intermediate forms as an isolated group, or as one or more subspecies or varieties of either sloe or damson, because of their different and variable phenotypes. It was found for instance that intermediates with identical stones mostly have a highly differentiated morphology (growth, foliage, wry or sweet fruits), whereas morphologically identical plants may produce different types of stones. The nature of this variation does not comply with the definition of any taxonomical group; (sub)species, varieties, populations etc. are similar or differ in fixed

characteristics. The variability found among the intermediates can only be expected in hybrids of diverse origin, and in the case of sloe and damson is probably the consequence of the wide range of specific *spinosa* and *insititia* varieties between which crossings may produce a great number of recombinations. The chance of obtaining F_1 types with unique properties in that case seems more probable than the creation of fully identical intermediate specimens. Indeed, in practice fully identical specimens are rare, if any occur at all.

Despite the morphological variation of fruits, leaves, growth, etc. in sloe and damson, written accounts emphasize the morphological invariability of the fruit stones in successive generations; in other words, the parent and its offspring will have morphologically identical stones, not only in self-pollinating, but also in cross-breeding lines. A significant implication of this mechanism is that the maternal plant as the producer controls the morphological configuration of the stones. There are indications that the mechanism works in the same way in crossings at species level (interspecific hybrids). A practical case, discussed by Hedrick (1911), concerns the beach plum, *Prunus maritima*, a low shrubby species from the east coast of the United States. The shrubs produce prolific crops, but the fruits are small and of an inferior quality. To improve the latter properties, the renowned Californian fruitgrower Burbank fertilized a selected *maritima* specimen with pollen of Japanese plums. A quotation: "The very first generation produces a plum which is an astonishing grower for a *maritima*, almost equal to *triflora*, with large, broad, glossy foliage almost of the exact shape of *maritima*, *maritima* blossoms, and fruits weighing nearly a quarter of a pound each, with an improved, superior *maritima* flavour, *maritima* pit in form, but enlarged".

The domination of maternal genes would explain the occurrence of intermediates with *spinosa* type stones and with *insititia* type stones. The different types of stones of the intermediates are very likely the result of crossings between different *insititia* and *spinosa* varieties. The dominance of the maternal plant in the formation of the stones in crossings would make it possible to identify the maternal plant, or variety involved in the parentage of the intermediates. The actual practice is mostly different. Owing to the number of varieties, and the small variability and size of *spinosa* stones, it is not possible to deduce specific varieties or strains from the features of intermediate stones. Stones of *insititia* varieties display more differentiation owing to their larger size, and more diverse shape and surface sculpture. This makes it possible in some cases to trace an intermediate's ancestry from the characteristics of its stones. The author compared types of stones of intermediates with similar stone types of *insititia* varieties, which were apparently involved in their parentage (Woldring, 1993). Stones of four intermediate types appeared to be so similar to those of certain *insititia* varieties (viz. two local Dutch varieties ('kroosjes' and 'blauwtjes'), the 'St. Julien', and a 'Spilling') as to clearly indicate the involvement of these varieties in the origin of the hybrid. In regions where a specific *insititia* variety predominates one would expect this variety to be a main contributor in the parentage of the intermediates. Proof for this statement is not available. The region between Lormes and Avallon, in the northwestern Morvan, central France, is studded with the French damson variant, the 'St. Julien'. Curiously, none of the samples secured from supposed hybrid specimens in this area shows the typical morphology of a 'St. Julien' stone.

Also remarkable is the occurrence of specimens with stones of identical type, but which on account of the other morphological features should be divided into intermediates and true damsons. Such was found in a series of specimens from the above-mentioned Morvan region. Besides the identical stones in this series, some of the specimens show features of both sloe and damson, and have therefore been interpreted as intermediates, whereas other specimens display dominating features of damson plums. It seems as if this phenomenon particularly shows up in areas where plums and/or sloe are abundant. The presence of such intermediate specimens with identical stones and variable other characteristics is quite confusing, but on the other hand might equally point to hybridization.

According to the Mendelian rules, interspecific hybrids (F_1) of the same origin are similar and uniform, whereas the progeny of F_1 specimens will segregate into types which partly resemble the parent plants (P_1). On the other hand, Stebbins (1960) argues that in general back-crossing between hybrids and the parental species is much more likely (because of the greater number of the latter) than the chance of intercrossing hybrid specimens. Back-crossing also leads to types which in part resemble the original parent plants. Specimens with dominating *insititia* features like those from the Morvan might thus originate from back-crossing processes rather than from segregating progeny of F_1 specimens. This would not be so important, were it not that back-crossing may have a significant side effect, namely an exchange of genes or genomes between the parental species. This process is sometimes termed introgressive hybridization (Stebbins, 1960). Indicators of such introgression might be the *insititia* specimens with bitter, inferior fruits, which are frequent in France, but occur also in other parts of Europe (Shiskin, in: Komarov, 1941).

Hybridization and subsequent back-crossing, and possibly also segregating F_2 progeny, leads to the establishment of a variable aggregate of intermediates including types which approach the original parent species in likeness. Such hybrid swarms can be seen in

other woody members of the rose family (*Crataegus, Sorbus*). In undisturbed natural situations these hybrid groups are found where genetically different and geographically isolated populations come into contact or where ecologically different habitats occur side by side. The distribution of interspecific types of sloe and damson, which seems to concentrate in central and western Europe, might be an indication that damson only recently intruded into previously sloe-dominated areas.

The earliest palaeobotanical evidence of damson plums in Europe consists of fruit stones recovered from Swiss lake-dwelling sites (Heer, 1866). Palaeobotanists disagree whether these were indigenous plums, as has been suggested for Austria by Werneck (1961), or were introduced by migrating farmers. *Prunus institutia* is a light-demanding species; it does not thrive in forest. The clearance of woodland and the exploitation of the environment may have encouraged the expansion of indigenous plums or the escape and running wild of cultivated specimens. In France, seemingly spontaneous *insititia* plums are still found in substantial numbers in hedgerows near villages and waste places.

Disturbed habitats also support the light-demanding and pioneering sloe. Because of its thorniness and rapid reproduction from rootsuckers, this species was popular as a cattle fence and was planted on the ramparts of early towns. The open conditions developing since the Neolithic caused two related species to invade identical habitats, which greatly increased the chances of hybridization.

8.2. The genetic origin of damson plums

The results of the breeding tests (section 5.3) show striking differences between black-fruited *insititia* specimens and those with other fruit colours. In most cases the black-fruited specimens produce fertile seeds, which develop into normal, be it heterozygous plants, whereas green-, yellow- or red-fruited *insititia* specimens show a universal seed sterility or inferior and aberrant growth of seedlings. The latter might therefore represent hybrids between damson (for the stones) and a *Prunus* group with variously coloured fruits, probably domestic plums, but also *Prunus cerasifera* plums may be considered potential parents. The inability of these hybrids to produce viable progeny suggests a genetic distance or barrier between *insititia* plums and cultivated *domestica* plums or *cerasifera* plums. Apparently these groups represent genetically different units.

The above suggests a genetic separation between black-fruited *insititia* varieties and the multi-coloured *insititia* group. The heterozygous growth of black-fruited *insititias*, inferred from the breeding tests, can have its origin only in cross-fertilization between *insititia* varieties. The discovery of the pronounced differences in reproduction and growth between the two *insititia* groups may have important consequences and suggests that the group of black-fruited *insititia* varieties represents the original 'botanical' species, which morphologically and genetically does not depart significantly from its wild ancestors.

Table 3. Evolution of the different groups of plums.

Spinosa		(Black-fruited) *insititia Domestica*
Spinosa x *insititia*	=	Intermediates (hybrids)
Insititia x *domestica*?		Red/yellow/green-fruited *insititia* varieties

Zohary & Hopf (1988) conclude that *Prunus insititia* might have evolved from (polyploid specimens of) the *cerasifera-divaricata* complex, as *insititia* and *cerasifera-divaricata* intergrade and apparently intercross with one another. In addition they state that sloe, with its wry and small fruits, is isolated cytologically and reproductively from the *domestica-cerasifera-divaricata* complex. Hybrids between sloe and the complex would be sterile; a statement which is however countered by the results of the progeny tests of intermediates, performed by the author. These tests reveal a complex of fertile hybrid forms between sloe and damson. The present study also found that interspecific forms of damson and cherry plum are uncommon. Viable crossings between the latter species would be expected if damson plums indeed arose from hybridization between sloe and cherry plum, as Rybin (1936) concluded from his investigations.

The morphological resemblance of sloe and black-fruited damsons, the global characteristics of the fruit stones and the occurrence of hybrids indicate a close relationship between those two species. Contemporary flowering, the characteristic development of rootsuckers, and the pubescence of twigs and fruit stalks are further traits which sloe and damson have in common. These features do not occur or are of a different nature in the *cerasifera-divaricata* aggregate of Zohary & Hopf, which diametrically opposes the interrelated sloe/damson cluster to *cerasifera-divaricata*. These discrepancies imply that an evolution of *insititia/domestica* directly from the *cerasifera/divaricata* complex as suggested by Zohary & Hopf must be considered improbable. The absence of features of *cerasifera/divaricata* in *insititia/domestica* also suggests that *Prunus insititia* did not evolve from crossings between sloe and cherry plums as claimed by Rybin (1936), but could have evolved directly from (hexaploid?) *spinosa* specimens.

8.3. The geographic origin of damson plums

Unlike domestic plums, feral *insititia* specimens

maintain themselves quite easily in Europe. Seemingly natural occurrences are frequent. Climatic aspects also indicate that *insititia* plums are at home in Europe. Its range of distribution includes various climates, but it seems that the species prefers the temperate parts of Europe and western Asia. The (English) damson and bullace thrive in the cool and humid Atlantic climate of Britain, as do the mirabelles and other *insititia* varieties in temperate France. *Insititia* plums are highly adjusted to the continental winters of central Europe. They have survived mass destruction among plums in severe winters, e.g. the loss of almost all prune trees in Germany in 1860 (Jahn et al., 1861) and the large-scale devastation of domestic varieties in Austria in 1928/1929, 1940/1941 and 1956 (Werneck, 1961). This hints that prehistoric fruit stones reported for central Europe (Heer, 1866; Hopf, 1968; Werneck, 1958; Bertsch, 1947) concern this species. Interestingly, such early records are practically missing in western Asia, e.g. the Caucasus, the region where *insititia* plums are thought to have their roots. (Admittedly, *divaricata* plums and other *Prunus* species, at home in western Asia by nature, are also absent in early archaeobotanical assemblages.) Palaeobotanists (Hopf, 1968; Körber-Grohne, 1996) suggest that *insititia* was not indigenous but was introduced in central Europe by the Neolithic farmers. According to Zohary & Hopf (1988), who cite Werneck & Bertsch (1959), pre-Neolithic remains of carbonized stones discovered in the Upper-Rhine and Danube regions closely resemble the stones of present-day spontaneous *domestica* plums (= *Prunus insititia*?). According to Zohary & Hopf these finds suggest that *Prunus insititia* could have predated agriculture and should be regarded as an indigenous element in central Europe.

This food resource, whether present or introduced into central Europe, has certainly been taken into cultivation and improved by further selection. Wild archetypes may eventually have disappeared through destruction of their habitats, competition and merging with the newly husbanded forms, a process that has been ascertained in various wild plants of which domesticated forms became widespread. For instance, the wild form of olive is not exactly known. In France and Italy, a great number of semi-wild forms of apple and pear show fruits which to some extent depart from the small-fruited, wild specimens. These specimens apparently result from intercrossing with domestic relatives. On the other hand, it has been demonstrated by Körber-Grohne (1996) that modern fruit stones of the German 'Krieche' are identical to those found in excavations of Swiss lake-dwelling sites and other Neolithic sites, e.g. Ehrenstein (c. 4000 BC) in central Europe. The millennia-long unaltered stone morphology would lead one to consider this black-fruited plum to be (one of) the elementary wild form(s) of *insititia*, even though it is maintained now by cultivation.

8.4. The importance of grafting for the development of domestic plums

The genetic range of domestic plums and the fact that most varieties are self-incompatible (and thus need to be cross-fertilized to set fruit) readily give rise to new types. Liegel, an Austrian who lived in the 19th century, in his life obtained c. 50 new plum varieties from fruit stones, some of which still exist. Many of our modern commercial plums date from the 19th century and were found as chance seedlings in gardens and hedges, such as Reine Claude d'Ouillins, Reine Victoria and Diamond, or have resulted from breeding tests at nurseries, e.g. Czar, River's Early Prolific, Jefferson and Belle de Louvain. Bud sports, spontaneous mutations in body (somatic) cells, usually in buds or tips of shoots, are another source of new types, e.g. Purple Pershore, which is a budsport of the yellow-fruited Pershore. Most of these forms would be shortlived, if not a new method of propagation - grafting - had emerged in Roman times. Technically, grafting is the method by which a part of the desired plant, the graft or scion, is inserted upon a related (purposely selected) rootstock. If successful, scion and rootstock will unite and grow up as one plant. This method ensures replication of specific features and therewith the preservation and continuation of varieties. Crops are often increased by grafting. The discovery of grafting with its advantages has been an essential condition for the development of *domestica* varieties. Its importance is emphasized in the so-called *Pelzbuch* (Gottfried von Franken, 1380), a treatise on the various aspects of grafting.

But not all plums depend on grafting. It is interesting to note that most *insititia* varieties produce acceptable crops when grown on their own roots. This goes also for prunes (*Prunus domestica* var. *pruneauliana*) and some other *domestica* plums such as Pershore, Aylesbury prune and Warwickshire drooper, varieties which are simply raised from rootsuckers. This method of reproduction might in part explain the expansion of *insititia* plums since the Neolithic era.

Grafting usually does not produce new fruit types, even though there are some examples of 'grafting hybrids', such as the two Crataegomespilus species, which arose from the union of *Mespilus* grafted on the rootstock of *Crataegus* (*C. dardari*, *C. asmieresii*; Boom, 1965). Most of the (often local) apple, pear and plum varieties have arisen from the age-long tradition of growing fruit trees from seed, a practice that is still successfully exercised by some people nowadays. In general, it is not possible to reproduce modern breeds from rootsuckers, cuttings or seeds, since these methods do not succeed or the plants produce poor yields and seedlings do not have the desirable qualities of the

parent plants. In these cases grafting has proved to be an adequate method of reproduction.

8.5. The value of written historical evidence

Roman written accounts point to Syria as the place where damsons (damason, damascenes: from Damascus), but also mirabelles (*Prunus insititia* ssp. *cerea*) and greengages or Reine Claudes (*Prunus domestica* ssp. *italica*) were thought to have originated. At present, plums are extensively cultivated in the coastal areas of Syria. Further inland, arid conditions in the growing season prohibit plum cultivation (Damascus average rainfall <200 mm per year). At the time of Roman hegemony in this area, various fruit types including the plum varieties mentioned by Pliny (23-79 AD; see Roach, 1985: p. 145) were introduced in Rome[1], where fruit growing was a popular hobby among prominent Romans. Marcus Lerentius Varro (116-27 BC) delightedly notes that the former woodland is so bestrewn with fruit trees from the Orient (Greece, Syria) in his time, that the landscape resembles a large fruit garden (Reinhardt, 1911: p. 86).

There are various statements by Roman writers on plums. Some of these raise questions about the taxonomy of the Roman damascenes, in the sense that these probably differed from the modern damsons which belong to the *insititia* group. The statements of Pliny on the conservation of damascene plums make it clear that these plums were preserved by drying in the sun, but, judging by the texts, with indifferent results - "they miss the sun of their homeland" - and concerning quality - "the fruits have larger stones and are less fleshy than in their homeland". Another author comments: "The best sorts of plums are damascenes, this testimony of Syria" (in: Reinhardt, 1911). At present the French 'St. Julien' is the only known *insititia* variety that can be suitably dried (like prunes). Of course, comparison of aspects such as taste remains hazardous; the perception of taste in Roman times probably greatly differed from ours. Comments as - 'the best sort of plums' - may indeed refer to conserving properties, but taking one thing with another, the descriptions of damascenes in Roman texts do not evoke the small and inferior *insititia* plums!

English historical records mention various authors/ fruit growers, e.g. Gerard (16th cent.), Evelyn (17th cent.), Hogg (19th cent.), who distinguish between 'Damasq' or 'Damaszen Plums' and damson varieties (Greenoak, 1983: p. 80), which suggests different groups.

Cherry plum is another frequently cultivated *Prunus* species in the western part of Syria. According to Post (1932) it is also found wild in hedges. Cherry plums thrive in the warm (sub-)Mediterranean climate, e.g. in western Anatolia, where the species in places dominates the arboreal vegetation of forest steppes. Husbanded and seemingly natural specimens are frequent in the Mediterranean climate zone of Greece and Italy. This plum probably spread in southern Europe through cultivation, possibly contemporarily with the so-called damascenes. It is not mentioned specifically in Roman accounts, even though it is in some respect superior to damson. The plants are extremely disease-resistant and are early and prolific croppers. Several strains produce excellent fruits. Disadvantageous (in northern countries) is its early flowering, which means that the flowers are often subject to frost damage.

Prunus insititia and *P. cerasifera* show much likeness. Authoritative researchers (compare Körber-Grohne, 1984; 1992) initially had difficulty separating the species. Even pomologists of the Noordelijke Pomologische Vereniging, who trace old fruit varieties in the Netherlands and are used to identifying fruit forms with minor differences, occasionally confuse forms of damson and cherry plum. It is possible that the Romans did not distinguish these plums as different groups. We may assume that part of the plums mentioned in Roman accounts belong to the *cerasifera* group, such as the so-called barley plum (*Prunus 'hordearium'*). According to Theophrastus this plum was so named because it ripens at the time of the barley harvest, approximately May-June. In the Mediterranean, only cherry plums ripen so early.

Questions are raised also by the Roman 'wax plum', a type thought to be identical with the modern mirabelle. If this is true, it would be one of the oldest known varieties. At present, the mirabelle is classified as a subspecies or variety of *Prunus insititia*, but some authors (Hegi, 1906 ff.) assume it to be a hybrid between plum and cherry plum. Indeed, leaves, fruits and growth of the mirabelle show much resemblance to (yellow-fruited) forms of cherry plums. It is not impossible that the noun 'myrobalan', a common synonym for cherry plums, and 'mirabel' became confused in later translations of Latin texts. Written records are almost the only information on fruit cultivation in ancient Rome. In contrast to the ample written documentation, archaeobotanical evidence such as fruits or seeds is virtually lacking in Roman Italy.

9. CONCLUSION

Results of breeding tests by the present author lead to the following conclusions (table3):

1. The intermediate forms (*Prunus* x *fruticans* in the *Flora Europaea*) investigated in this study are mostly hybrids of *Prunus spinosa* x *P. insititia*. These crossings are usually fertile and imply a close relationship between the parent species;

2a. As a rule, black-fruited *insititia* varieties readily produce viable progeny from seed. By contrast, seed sterility or growth deficiencies are common in *insititia*

forms with other fruit colours;

2b. It is inferred from these data (2a) that black-fruited *insititia* specimens form the original species. *Insititia* specimens with differently coloured fruits probably result from hybridization between *insititia* and other groups of plums, e.g. *domestica*;

3. The relationship between *spinosa* and *insititia* is manifested in the frequency of intermediates, the morphological resemblance of the fruits, identical (often shrub-like) growth, synchronic flowering, luxuriant development of rootsuckers, etc. This suggests that *Prunus insititia* evolved from certain strains of *Prunus spinosa*. There are no indications for the involvement of cherry plums in the development of *insititia* plums;

4. The constancy of many *domestica* plums depends on grafting, since seedlings produce plants with different qualities. Seed sterility and low viability of many *domestica* varieties suggest heterozygosity and an origin from genetically different groups. Crossings between *insititia* varieties may have been the principal ancestry of *domestica* varieties.

The conclusions mentioned here are strongly based on the results of the breeding tests. The underlying idea in undertaking this project, the comparison of fruits and fruit stones of seedlings with those of the respective parent plants, is still to be worked out. With the exception of a number of cherry plum seedlings, most offspring of the other *Prunus* species and intermediates has not yet fruited. The author hopes to present the results of this research in a future paper.

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11. GLOSSARY OF TECHNICAL TERMS

Bloom
: Waxy layer on the surface of *Prunus* fruits, giving the impression of a blue or whitish coloured fruit

Citric acid
: Chemical component causing the sour taste of e.g. oranges and grape fruits

Dorsal/ventral suture
: Opposite sharp-angled parts of the fruit stone. The ventral suture runs parallel and is located at the same side as the line of junction visible on the exterior of the fruit

Chromosomes
: Linear bands in cells that carry the genes

Cross/self-fertilization
: Fusion of male and female gametes. Self-fertilization is the fusion of male and female gametes from the same individual

F_1
: The first filial generation

Fruit stones
: The pits or seeds of *Prunus* fruits

Gamete
: Haploid reproductive cell

Genus
: Taxonomic group of closely related species. Genera are grouped into families

Gen
: Basic unit of inheritance by which hereditary characteristics are transmitted from parent to offspring

Genome
: The haploid genetic set of a living (diploid) organism

Grafting
: Insertion of scion (graft) onto stock, usually of an other organism

Homologous chromosomes
: Contain the same sequence of genes, but derived from different parents

Large-fruited
: Indicates specimens with the normal morphology of the type species, but with larger fruits as the type species

Pedicels
Fruit stalks

Polyploid
Plants having more than two chromosome sets persomatic (body) cell

Prunes
Group of domestic plums with specific drying qualities. Typical varieties: German prune ('Zwetsche'), 'Stanley', 'Prune 'd Ente (d'Agen)', 'Italian prune', 'Hungarian' (date) plum. The term 'prune' is used here to distinguish the group from other domestic plums.

Species
Taxonomic unit which normally does not interbreed with other such groups; related species are grouped into genera

Variety
Taxonomic group below the species level

12. NOTE

1. The sharp increase of plum, apple and pear varieties in Pliny's time, the first century AD, is not necessarily due to the introduction of 'foreign' varieties in Rome. The Romans' passion for fruit growing must have led to the development of new fruit varieties. A recent equivalent of rapid accumulation of varieties is found in the very young States of America, where plum cultivation started c. 1750. By 1828, Prince Nurseries, New York, were offering 140 plum varieties for sale, including several American varieties!

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APPENDIX 1. Intermediate forms of *Prunus insititia* and *Prunus spinosa*.

In this Appendix, *Prunus* forms intermediate to *insititia* and *spinosa* are described and depicted. The selection of the specimens is based on the characteristics of the stones; each specimen represents a different type of stone. Locations of specimens with identical stones are mentioned under the type-specimen.

The type description includes location, date of collection, habitat, character and measurements of the tree/shrub, leaves, pedicels, fruit and fruit stones. In many cases measurements of leaves of summer shoots and the fruit-bearing lateral spurs are indicated separately. Some of the types were used in the breeding tests. Where this is the case, germination and growth rate are indicated.

The tables present the average, minimum and maximum measurements of length, thickness and breadth of the fruits and fruit stones. The dimensions of fruits and fruit stones show much overlap, for which reason proportional indices have been omitted. The measurements of fruits and stones of modern *insititia* varieties presented in Van Zeist and Woldring (this volume) may serve as a reference.

Owing to their fairly similar appearance (usually black to purple or bluish colour, round or almost round-shape), black-and-white photographs of the fruits also were deemed to be of little value.

HELP.Z-92-1: Helpman, suburb of the town of Groningen, the Netherlands, September 1992
Small-sized tree with many root suckers in planting alongside road, height c. 4 m. Leaves almost circular to obovate, 7x4.5 cm. Summer shoots glabrous. Fruits subglobose with much bloom. Taste sweet but not pleasant. Pedicels smooth, length 5-10 mm, diameter c. 1.0 mm. General impression of *insititia*, but shape of the plums resembles *spinosa*. *Spinosa*-type stones. Germination rate c. 70%, seedlings fairly homogeneous. Moderate growth.

VAG-91-2: Nietap, province of Drenthe, the Netherlands, 5th September 1991
Large shrub with few stems and many rootsuckers, height up to 5 m. Summer shoots thinly pubescent. Leaves quite large, oval to elliptic, 7x4 cm. Fruits almost round to oval, drooping, blackish, glossy. Taste wry. Pedicels thinly pubescent to glabrous, length 8-18 mm, diameter unknown. *Insititia* features: general fruit characteristics, leaves. *Spinosa* features: stones, wry fruits, habitus(?). Germination rate 20%. Seedlings display heterogeneous growth.
NB. In newly planted, c. 25-year-old forest, but possibly part of a former hedgerow. A second specimen, with different stones (not shown), grows at a distance of only 50 m. This specimen flowers abundantly each year, with large *insititia*-type flowers (diameter 2.5 cm), but fruit setting is extremely poor.

DOM-95-1: Domecy-sur-Cure, Morvan, France, 31st August 1995
Many-stemmed shrub in front of the local château, as broad as high, c. 3 m. Summer shoots smooth. Leaves oval to elliptic, 6x3.5 cm at maximum. Fruits slightly drooping, overspread with thick bloom, round to subglobose, sweet and tasty, free stone. Pedicels thinly pubescent to glabrous, length 9-14 mm, diameter 1.0-1.1 mm. *Insititia* features: leaves, taste of fruit. *Spinosa* features: stones, habitus, bloom?

BARN-96-1: Barnsley, Cotswold Hills, Gloucestershire, Great Britain, 8th September 1996
Productive shrub in a hedgerow dominated by sloe, height 3 m. Summer shoots pubescent. Leaves oval, c. 4x2.5 cm. Leaves of fruit spurs larger(!), oval (sometimes obovate), c. 4.5x3 cm. Fruits round, drooping. Taste sugary, free stone. Pedicels glabrous, length 4-11 mm, diameter 1.1-1.3 mm. *Insititia* features: fruits. *Spinosa* features: stones, leaves.
NB. Another specimen with the same type of stones (BARN-96-2) has leaves identical to *spinosa* leaves.

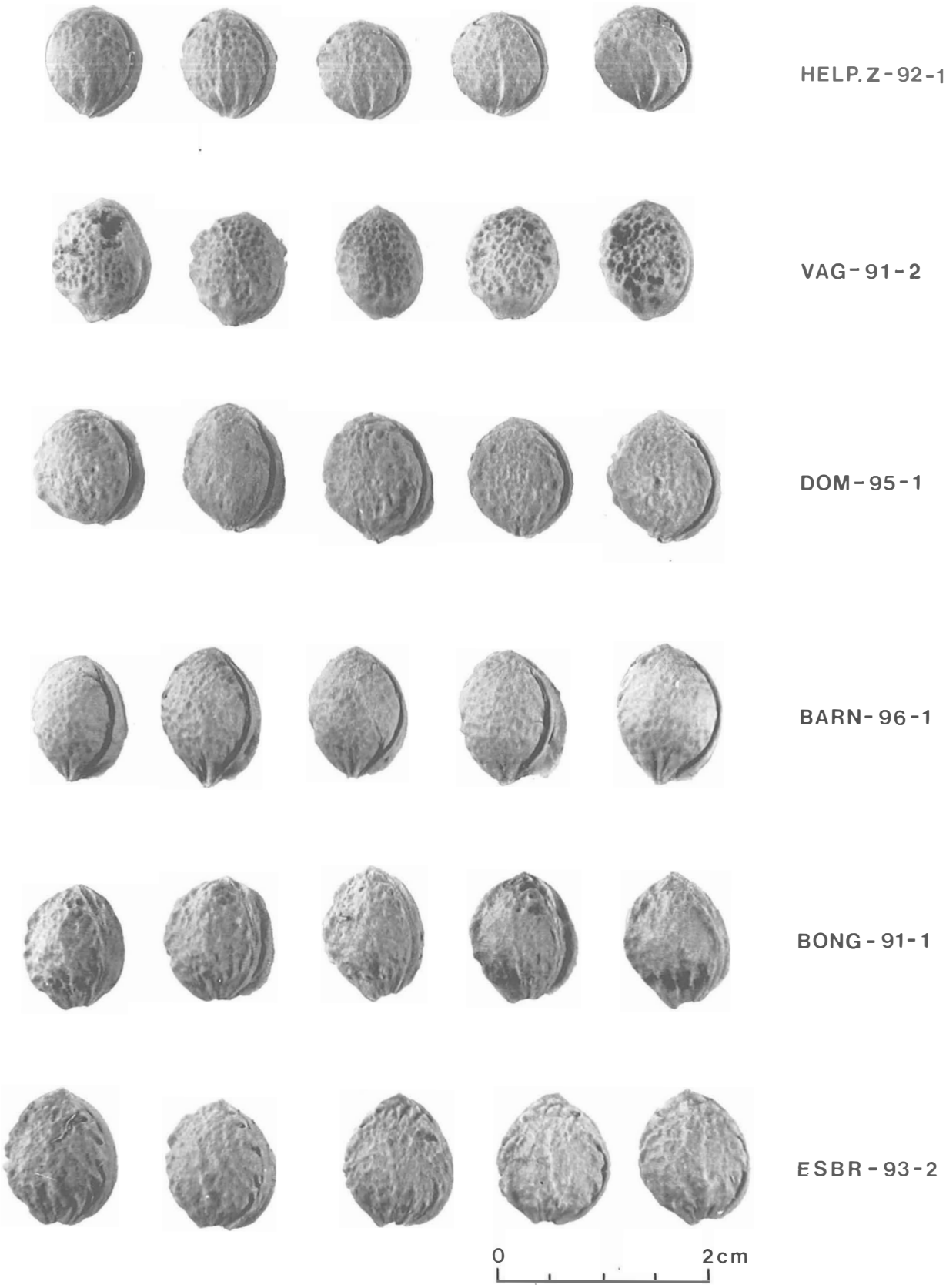
BONG-91-1: Bunnerveen, near Peize, province of Drenthe, the Netherlands, 28th September 1992
Old plantings between sandy track and arable land. Small to medium-sized tree with abundant secondary, extremely spiny vegetation, height c. 4 m. Summer shoots pubescent. Leaves appr. oval, 4-4.5x3-3.5 cm. Leaves of lateral spurs oblanceolate-obovate, 3-4x1.6-2.3 cm. Fruits oval, more or less drooping, with or without bloom. Taste very acid. Pedicels thinly pubescent, length 7-11 mm, diameter 0.8-1.2 mm. *Insititia* features: fruits. *Spinosa* features: size and arrangement of leaves, habitus. Stones with predominantly *spinosa* features.

ESBR-93-2: Esbruyère, between Arnay-le-Duc and Autun, Côte d'Or, France, 3rd September 1993
Next to SPIN-ESBR-93-1, from which it might be a seedling (originating from fertilization with *insititia* pollen). Both specimens located in pasture. Shrub with five stems, height c. 3 m. Summer shoots pubescent. Leaves obovate, 4-6.5x2.3-3.5 cm. Leaves of lateral spurs lanceolate (small ones) or obovate (larger ones), 2.5-6x2.3-3.5 cm. Fruits almost round, drooping. Taste acid to wry. Pedicels almost smooth, sometimes in pairs, length 7-12 mm, diameter 1.0-1.5 mm. *Insititia* features: fruits, leaves. *Spinosa* features: stones, taste of fruits. Germination rate c. 60%. Seedlings display homogeneous growth. Indices fruits: B/L.100=104, T/L.100=98, T/B.100=94; indices stones: B/L.100=56, T/L.100=84, T/B.100=151

	HELP.Z-92-1	VAG-91-2
Fruits		
Number	15	12
Length	16.6(15.5-17.7)	17.5(14.5-20.5)
Thickness	18.1(16.5-19.4)	16.7(14.0-19.1)
Breadth	18.8(17.4-20.2)	17.5(14.5-21.3)
Stones		
Number	23	24
Length	9.8(9.0-10.9)	10.5(9.2-12.0)
Thickness	8.6(8.0-9.4)	8.3(7.0-9.6)
Breadth	6.7(6.3-7.2)	6.3(5.6-7.1)

	DOM-95-1	BARN-96-1
Fruits		
Number	10	16
Length	19.8(19.0-21.1)	20.9(18.5-23.1)
Thickness	20.0(18.0-21.3)	19.7(17.7-21.9)
Breadth	20.2(18.0-22.5)	20.5(18.3-23.0)
Stones		
Number	20	15
Length	12.0(10.7-13.0)	12.7(11.7-13.7)
Thickness	9.7(8.7-10.8)	9.4(8.8-10.1)
Breadth	6.7(6.1-7.3)	7.4(6.9-8.8)

	BONG-91-1	ESBR-93-2
Fruits		
Number	11	20
Length	18.1(17.1-19.9)	18.7(16.2-20.9)
Thickness	16.6(15.6-18.1)	18.3(15.7-19.7)
Breadth	16.7(15.4-18.4)	19.5(16.5-21.3)
Stones		
Number	19	25
Length	12.5(11.4-13.6)	12.7(11.5-13.7)
Thickness	9.8(8.7-10.8)	10.7(9.5-11.6)
Breadth	6.3(5.7-7.3)	7.1(6.5-7.6)


HELP.Z-92-1
VAG-91-2
DOM-95-1
BARN-96-1
BONG-91-1
ESBR-93-2
0
2cm

SPIN-ESBR-93-1: Esbruyère, between Arnay-le-Duc and Autun, Côte d'Or, France 10th September 1993
Next to ESBR-93-2, spreading shrub, not very spiny, height c. 3 m. Summer shoots pubescent. Leaves oblanceolate-elliptic-obovate, length c. 4x1.5-2.0 cm. Leaves of lateral spurs (ob)lanceolate, 3-5x1.0-1.8cm. Fruits round, non-drooping. Taste wry. Pedicels smooth, length 4-5 mm, diameter 0.9-1.0 mm. Indices fruits: B/L.100=102, T/L.100=98, T/B.100=96; indices stones: B/L.100=64, T/L.100=84, T/B.100=132
NB. Indices of fruit and fruit stones show remarkable correspondence with ESBR-93-2, whose (maternal) parent this *spinosa* specimen is assumed to be.

GERAUD-92-1: La Chapelle Saint Geraud, Dordogne, France, 5th September 1992
Slender, spinescent shrub in hedgerow, height c. 5 m. Summer shoots densely pubescent. Leaves elliptic to oval, 9x5 cm or smaller. Fruits appr. round, drooping. Taste acid. Pedicels pubescent, length 4-8 mm, diameter 1.0-1.2(1.5) mm. *Insititia* features: drooping, large fruits. *Spinosa* features: stones, leaves, spinescence.

GIE-90-2: Gieten, province of Drenthe, the Netherlands, 31st July 1990
Spiny shrubs and rootsuckers over tens of metres under tall oaks, height 2-3 m. Summer shoots sparsely pubescent. Leaves oval, 6x4.5 cm. Some dead stems occur with a diameter of c. 10 cm at 1 m height. Flower diameter c. 2.5 cm, fruits resemble large sloe fruits, semi-drooping. Taste wry. Pedicels smooth, length 8-13 mm, diameter 0.8-1.3 mm. *Insititia* features: leaves. *Spinosa* features: habitus, type and taste of fruit. Germination rate 50%. Seedlings display vigorous homogeneous growth.
NB. The characteristics of the Gieten specimen, in particular those of the stones, suggest an origin from a crossing of 'kroosjes' and sloe (cf. Woldring, 1993).

GIE-91-4: Gieten, province of Drenthe, the Netherlands, 22nd October 1991
Shrub with few rootsuckers at the edge of a forest (chiefly oaks) and plantation of spruce, height c. 3 m. Summer shoots pubescent. Leaves elliptic-oval, 5-7x2.5-5 cm. Fruits resemble GIE-90-2, but slightly more oval, slightly drooping. Taste acid. Pedicels pubescent, length 7-13 mm, diameter 1.0-1.4 mm, stones resembling the previous type. *Insititia* features: fruits, leaves. *Spinosa* features: shrubby growth. Germination rate 100%. Seedlings display mostly homogeneous, moderate growth. Stones with predominantly *spinosa* features.

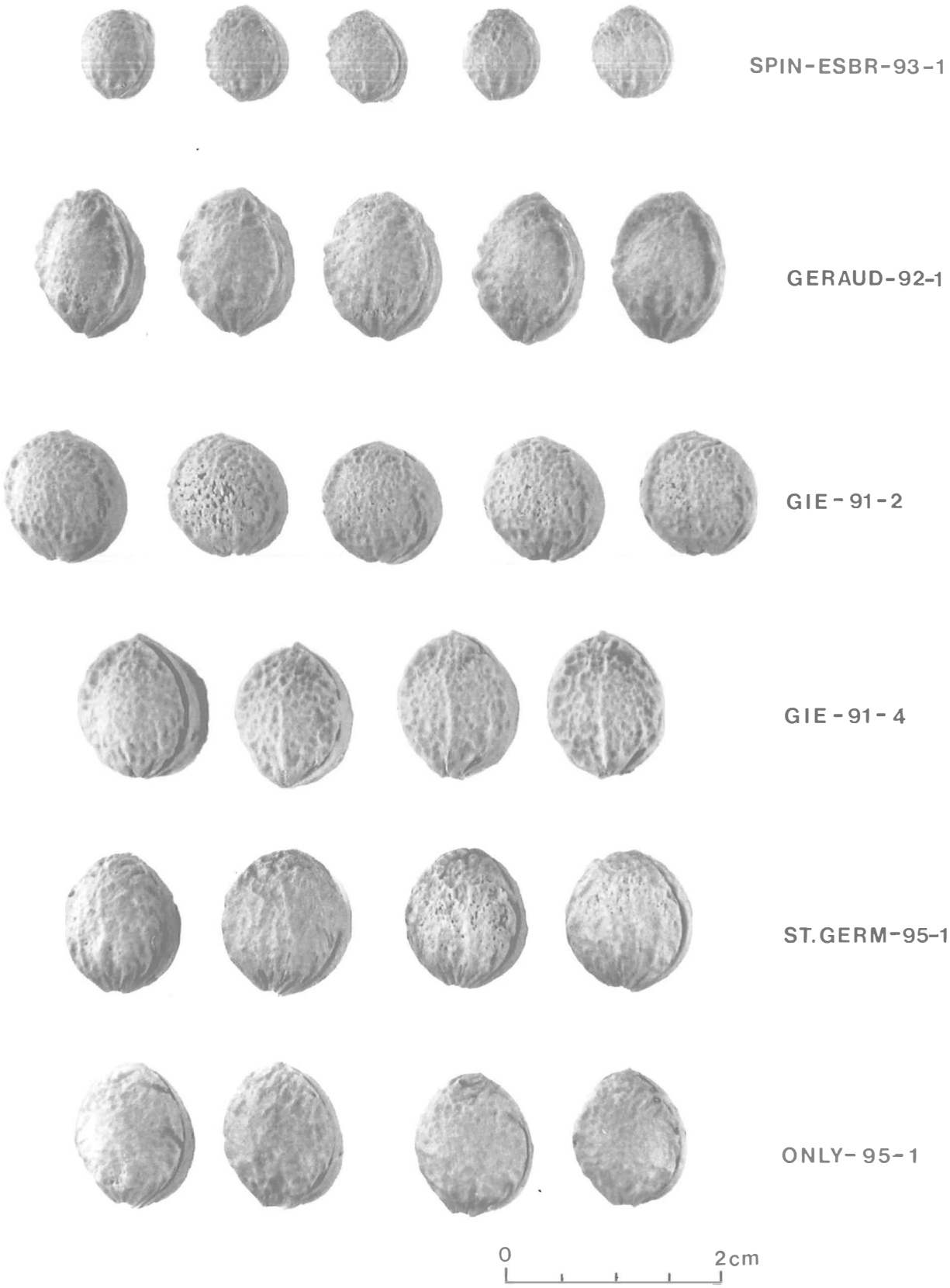
ST.GERM-95-1: St. Germain des Champs, Morvan, France, 31st August 1995
Large, very productive tree in hedgerow between meadows, height 6-7 m. Summer shoots pubescent. Leaves oblanceolate-obovate, 5.5x3.3 cm at maximum. Leaves of lateral spurs smaller, elliptic to (ob)lanceolate. Fruits round, drooping. Taste wry. Pedicels glabrous, also in pairs, length 9-15 mm, diameter 1.0-1.2 mm. *Insititia* features: habitus, size of fruits. *Spinosa* features: leaves, stones, taste of fruits. Types with identical stones: Esbruyère, Dracy Chalas (Côte d'Or), Brazey-en-Morvan, Dalmazane (Dordogne), possibly also Rasquert (Groningen, the Netherlands). Most common type of stone in the intermediates.

ONLAY-95-1: Onlay, Morvan, east-central France, 7th September 1995
Two identical trees near the village, height c. 5m. Summer shoots glabrous. Leaves oval, 7x5.5 cm or smaller. Fruits globular, drooping. Taste sweet. Pedicels mostly glabrous, length 7-10 mm, diameter 1.0 mm. *Insititia* features: size and taste of fruits, habitus and size of trees, leaves. *Spinosa* features: stones.

	SPIN-ESBR-93-1	GERAUD-92-1
Fruits		
Number	15	11
Length	13.8(12.5-14.8)	24.8(22.5-27.8)
Thickness	13.5(12.8-14.1)	22.6(19.7-26.0)
Breadth	14.1(12.9-15.1)	24.2(21.2-27.4)
Stones		
Number	25	20
Length	8.8(8.1-9.4)	14.3(12.6-15.3)
Thickness	7.4(6.7-8.1)	10.5(8.6-11.4)
Breadth	5.6(5.0-6.2)	6.8(6.4-7.3)

	GIE-90-2	GIE-91-4
Fruits		
Number	16	12
Length	18.6(15.0-21.0)	26.1(22.7-28.8)
Thickness	18.2(14.8-20.3)	24.6(21.2-27.3)
Breadth	18.4(15.2-21.1)	25.6(21.5-28.2)
Stones		
Number	26	25
Length	12.7(11.5-14.1)	14.7(13.5-16.6)
Thickness	11.3(9.9-12.4)	12.5(11.1-14.4)
Breadth	7.8(6.5 -8.9)	8.5(7.7-9.3)

	ST.GERM-95-1	ONLAY-95-1
Fruits		
Number	10	11
Length	21.4(19.3-22.7)	20.5(17.5-23.2)
Thickness	20.5(17.7-21.9)	19.3(16.8-22.1)
Breadth	21.1(18.0-23.0)	20.3(18.5-22.9)
Stones		
Number	22	22
Length	13.3(12.2-13.9)	13.0(11.5-14.3)
Thickness	11.3(10.4-12.0)	10.5(9.2-11.4)
Breadth	8.5(7.7-9.3)	6.6(5.8-8.1)


SPIN-ESBR-93-1
GERAUD-92-1
GIE-91-2
GIE-91-4
ST.GERM-95-1
ONLY-95-1
0
2cm

LESS-94-1: Lessard-et-le-Chêne, Normandy, France, 7th September 1994
Medium-sized, somewhat spiny shrub with few rootsuckers at the edge of a garden, height almost 3 m. Summer shoots thickly pubescent. Leaves (oblanceolate) elliptic to obovate, 4-7x2.5-4 cm. Fruits round-truncate, drooping? Taste acid to sweet. Pedicels pubescent, length 7-14 mm, diameter 1.4-1.8 mm. *Insititia* features dominant, except for habitus and leaves.

MASS-92-2: Massalve, Dordogne, France, 3rd September 1992
Thickets at the fringe of forest and meadow, forming a hedgerow over tens of metres, up to 5 m in height. Summer shoots densely pubescent. Leaves oval to broad elliptic, appr. 5x3 cm. Fruits subglobose to round, large, bloom not removable. Taste acid to wry. Pedicels pubescent, often in pairs or in clusters, length 6-13 mm, diameter 1.1-2.2 mm. *Insititia* features: drooping, large fruits. *Spinosa* features: stones, taste of fruits, habitus, leaves. Germination rate 50%. Seedlings display slightly heterogeneous growth.

ST.MARIE-94-1: Sainte Marie-en-Anglais, Normandy, France, 31st August 1994
Shrub on short stem, cultivated in garden, height 2m, breadth c. 2 m. Summer shoots thickly pubescent. Leaves uniform oval to almost circular, 3x2.5 cm. Leaves of lateral spurs elliptic or lanceolate, 2-4.5x1.0-2.0 cm. Fruits round, semi-drooping, bloom. Taste wry (but not very ripe). Pedicels pubescent, length 4-6 mm, diameter 1.2-1.9 mm. *Spinosa* features in every aspect, except for the extremely large fruits and stones. Might be a 'macrocarpa' form or result from cultivation.
NB. Six round-topped shrubs, height c. 3 m, cultivated in a garden near Lassery, Monteille (Normandy) display identical morphological features, fruits and stones. Six stones of this type rendered three heterogeneous seedlings.

SERVE-93-1: Serve, between Arnay-le-Duc and Autun, Côte d'Or, France, 6th September 1993
Round-shaped, productive tree with shrubby rootsuckers, in (abandoned?) farmyard, height c. 4 m. Summer shoots pubescent. Leaves obovate, 8x3.5-4 cm. Leaves of lateral spurs 5-8x3-3.5 cm. Fruits slightly ovate, drooping. Taste acid to wry. Pedicels thinly pubescent, length 6-10 mm, diameter (1.2)1.4-1.5(1.8) mm. *Insititia* features: fruit arrangement, size of fruits, leaves. *Spinosa* features: stones, wry taste. Germination rate 85%. Homogeneous, vigorous growth of seedlings.

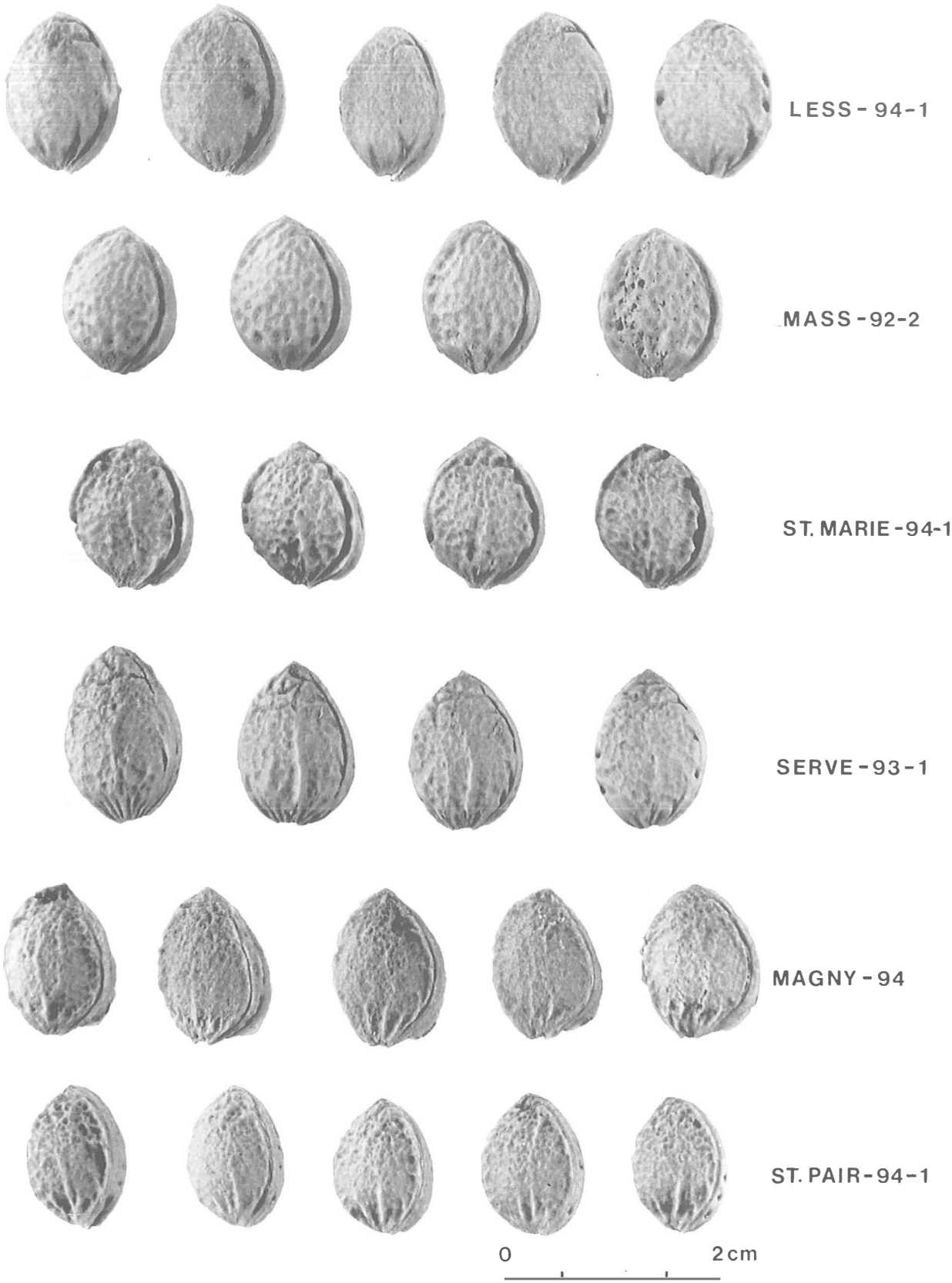
MAGNY-94: Magny-le-Freule, Normandy, France, 5th September 1994
Trimmed(!) spiny hedge over c. 20 m, between road and arable land, height c. 1,5 m. Summer shoots thickly pubescent. Leaves elliptic or obovate, 4-6.5x2.5-3.5cm. Leaves of lateral spurs (ob)lanceolate to elliptic, 2.5-5x1.0-3.0 cm. Fruits round, slightly drooping, thick bloom, fruit setting from about 30 cm above the ground. Taste sugary. Pedicels pubescent, length 3-9 (mostly 6) mm, diameter 1.3-1.8 mm. *Insititia* features: fruit characteristics, stones. *Spinosa* features: shrubby habitus (evident from some free-standing specimens), leaves.

ST.PAIR-94-1: Saint Pair du Mont, Normandy, France, 28th August 1994
Large, almost spineless tree with vigorous branches growing in a hedgerow, height c. 5 m. Summer shoots pubescent. Leaves appr. oval, c. 6x3.5 cm. Leaves of lateral spurs oblanceolate-obovate, 2.5-5x1.5-2.5 cm. Fruits roundish or truncate, drooping. Taste wry. Pedicels glabrous, length 6-10 mm, diameter 1.0-1.4 mm. *Insititia* features: stones, size of fruits, habitus. *Spinosa* features: leaves, taste of fruits.

	LESS-94-1	MASS-92-2
Fruits		
Number	16	11
Length	25.2(22.0-29.1)	27.5(25.3-29.5)
Thickness	22.3(19.0-25.6)	26.6(24.0-28.3)
Breadth	23.8(20.9-27.0)	28.5(26.0-30.2)
Stones		
Number	21	25
Length	15.0(12.9-17.5)	14.9(13.5-16.3)
Thickness	10.5(9.1-11.8)	11.3(10.1-12.1)
Breadth	6.9(6.2-7.5)	7.5(6.7-8.3)

	ST.MARIE-94-1	SERVE-93-1
Fruits		
Number	20	16
Length	20.3(17.4-23.4)	23.0(19.7-24.6)
Thickness	20.2(16.9-23.1)	21.0(17.8-22.6)
Breadth	20.5(17.0-23.3)	22.6(19.8-24.6)
Stones		
Number	23	25
Length	12.9(10.7-14.6)	15.1(12.9-16.1)
Thickness	10.5(8.2-12.0)	11.1(9.6-11.9)
Breadth	7.0(6.0-8.2)	7.8(6.7-8.8)

	MAGNY-94	ST.PAIR-94-1
Fruits		
Number	15	15
Length	22.6(20.1-24.1)	20.1(18.1-22.4)
Thickness	21.2(19.1-23.8)	18.1(16.7-19.4)
Breadth	22.0(19.8-25.1)	19.3(17.4-20.7)
Stones		
Number	19	24
Length	14.6(13.5-15.5)	13.1(11.3-14.7)
Thickness	10.4(9.3-11.5)	9.2(8.2-10.0)
Breadth	7.7(6.9-8.6)	6.5(5.6-7.2)


LESS - 94-1
MASS - 92-2
ST. MARIE - 94-1
SERVE - 93-1
MAGNY - 94
ST. PAIR - 94-1
0
2 cm

LASS-94-3: Lassery, near Monteille, Normandy, France, 31st August 1994
Small-sized, almost spineless tree with some rootsuckers, in hedgerow, height 3-4 m. Summer shoots pubescent. Leaves elliptic to (ob)lanceolate, c. 3×1.5 cm. Leaves of lateral spurs almost the same size. Fruits oval, drooping, thickly bloomed. Taste wry. Pedicels pubescent, length 4-8 mm, diameter 1.1-1.5 mm. *Insititia* features: size of fruits and stones, habitus. *Spinosa* features: sculpture of stones, leaves, taste of fruits.

PONC-93-1: Poncey, between Arnay-le-Duc and Autun, Côte d'Or, France, 5th September 1993
Spiny shrubs in hedgerow between *spinosa* specimens, at the edge of a meadow, many rootsuckers, height up to 3 m. Summer shoots thinly pubescent. Leaves elliptic-obovate, 5×2.5 cm. Leaves of lateral spurs oblanceolate, 3-4.5×1.6-2.5 cm. Fruits drooping, ovate, sometimes oval. Taste wry. Pedicels glabrous, length 6-9 mm, diameter 0.9-1.2(1.4) mm. *Insititia* features: stones, most fruit characteristics. *Spinosa* features: leaves, habitus, taste of fruits. Germination rate 50%. Seedlings display homogeneous growth.

LAB-92-1: Laboureyrie, south of Le Pêcher, Dordogne, France, 11th September 1992
Shrub in hedgerow, height c. 3 m. Summer shoots smooth. Leaves elliptic to oval-obovate, 7×3.5 cm at maximum. Leaves of lateral spurs smaller, elliptic-lanceolate. Fruits drooping, subglobose. Taste sweet. Pedicels almost smooth, sometimes in pairs, length 5-12 mm, diameter 1.0-1.5 mm. *Insititia* features: fruits. *Spinosa* features: stones, habitus, leaves. Specimens with identical stones: St.-Julien-Maumont, Dordogne; St.-Pair-du-Mont, Normandy, France.

LEUT-91-1: Leutingewolde, province of Drenthe, the Netherlands, 5th October 1991
Shrub with many rootsuckers, in hedgerow alongside road, height c. 3 to 4 m u. Leaves elliptic to lanceolate, 6×2.5-3 cm. Fruits ovate. Taste wry. Pedicels smooth, length 5-10 mm, diameter 1.1-1.6 mm. Except for the size of the fruits, features of sloe predominate. Large-fruited form of sloe? Germination rate c. 50%. Seedlings demonstrate homogeneous, quite vigorous growth. A specimen with identical stones was found in a plantation in the nearby village of Peize.

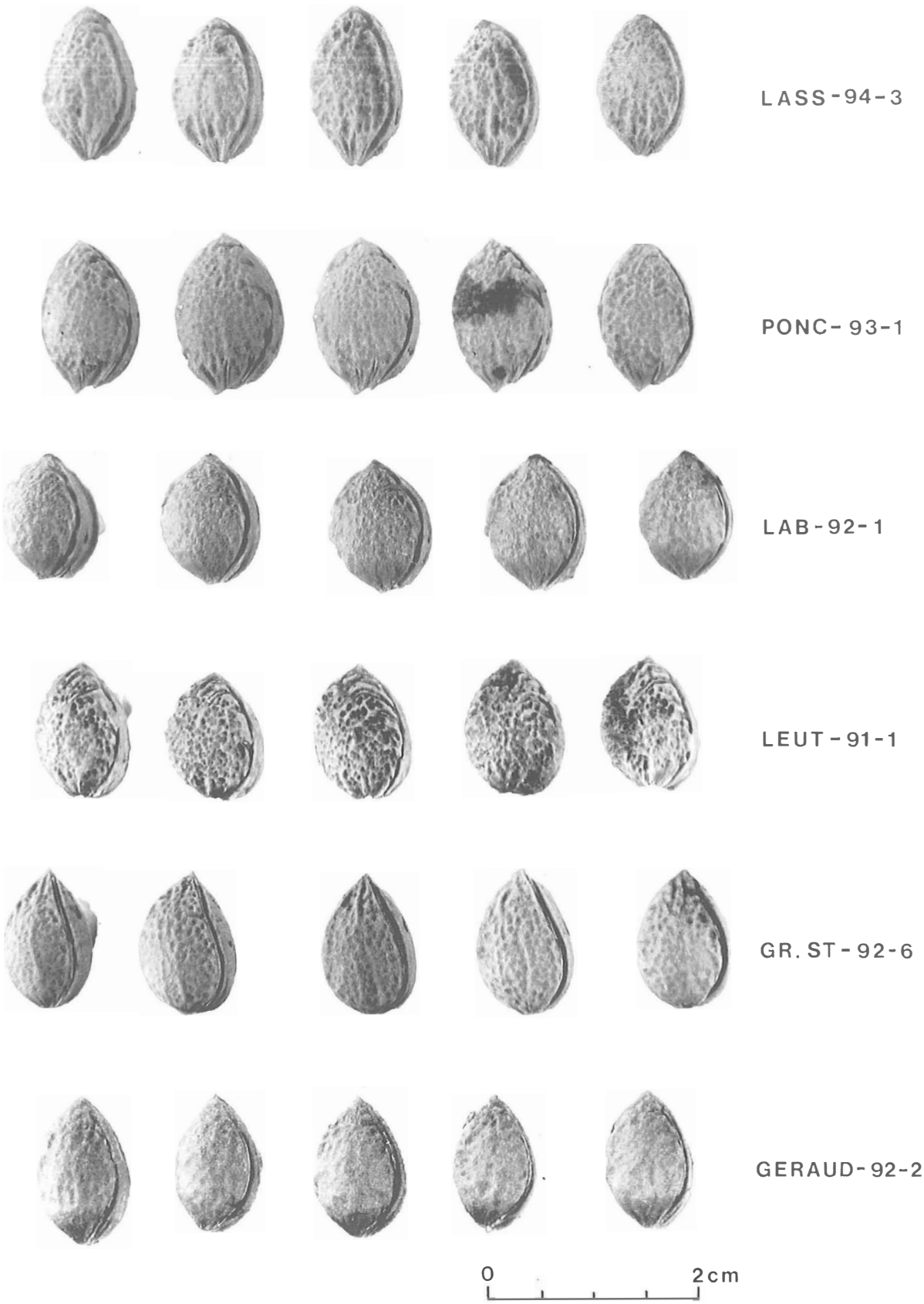
GR.ST-92-6: Groningen 'Stadspark', the Netherlands, 18th August 1992
Many-stemmed spiny shrub, with many rootsuckers, height c. 4 m. Summer shoots pubescent. Leaves oval, 8×4-4.5 cm. Fruits ovate, blackish-brown. Taste acid to wry. Pedicels length 11-15 mm, diameter 1.3 mm. *Insititia* features: leaves, large drooping fruits. *Spinosa* features: shrub habitus, taste of fruits, stones(?) Three specimens with similar stones were found in the park.

GERAUD-92-2: La Chapelle Saint Geraud, Dordogne, France, 5th September 1992
Small-sized tree in garden, height c. 3 m. Summer shoots sparsely pubescent. Leaves oblanceolate-elliptic, 6×3 cm at maximum. Fruits drooping, ovate to oval. Taste sweet/sugary. Pedicels in pairs, pubescent, length 5-9 mm, diameter 1.1-1.4 mm. Stones identical to a specimena in the nearby hamlet of Croisille, Dordogne, France.

	LASS-94-3	PONC-93-1
Fruits		
Number	14	17
Length	22.5(18.3-24.6)	21.8(20.3-24.0)
Thickness	19.3(14.7-21.2)	18.6(17.2-21.4)
Breadth	20.3(16.1-22.3)	19.7(17.9-22.6)
Stones		
Number	14	25
Length	14.1(11.6-15.6)	15.1(13.7-16.3)
Thickness	8.8(7.0-9.3)	9.9(9.2-10.8)
Breadth	6.2(4.9-6.9)	6.4(5.8-6.8)

	LAB-92-1	LEUT-91-1
Fruits		
Number	15	20
Length	21.9(20.7-23.7)	17.1(15.5-18.4)
Thickness	22.8(21.8-24.3)	16.1(15.1-18.0)
Breadth	23.5(22.2-25.2)	16.8(15.2-17.8)
Stones		
Number	22	20
Length	11.9(11.0-13.1)	12.9(11.7-13.8)
Thickness	9.3(8.7-10.0)	9.4(8.4-10.0)
Breadth	6.0(5.6-6.7)	6.7(6.0-7.4)

	GR.ST-92-6	GERAUD-92-2
Fruits		
Number	11	10
Length	19.6(18.1-21.1)	24.5(23.4-26.6)
Thickness	17.0(15.3-18.0)	21.9(19.8-25.0)
Breadth	17.6(15.8-18.5)	23.2(21.3-24.4)
Stones		
Number	22	21
Length	13.4(11.8-14.5)	13.8(13.0-14.8)
Thickness	9.0(8.0-10.1)	8.6(8.0-9.3)
Breadth	6.3(5.7-7.0)	6.4(5.9-7.6)


LASS-94-3
PONC-93-1
LAB-92-1
LEUT-91-1
GR. ST-92-6
GERAUD-92-2
0
2cm

ST.ROM-95-2: Saint Romain, near Beaune, Côte d'Or, France, 1995
Shrub on castle ramparts, height 2 m. Summer shoots pubescent. Leaves mostly obovate, some (ob)lanceolate, 2.5-5x1.3-3.0 cm. Fruits almost black, drooping, oval-ovate. Taste almost wry. Pedicels smooth, length 7-11 mm, diameter 1.0-1.4 mm. Mostly *insititia* features, except for its shrubby habitus and small stones. The leaves of this specimen are much smaller but similar in shape to a nearby-growing *insititia* specimen of the variety 'St.-Julien'.

ST.BONNET-92-1: Saint Bonnet near Sexcles, Dordogne, France, 3rd September 1992
Shrub, height unrecorded. Summer shoots pubescent. Leaves elliptic to almost oval, 5x2.5-3.5 cm. Fruits roundish with bloom. Taste sweet with acid aftertaste. Pedicels pubescent, length 6-9 mm, diameter 1.0-1.4 mm. *Insititia* features: taste and size of fruits. *Spinosa* features: stones, leaves, habitus. Identical type: Le Pêcher, Dordogne, France.

LE PECH-92-1: Le Pêcher, Dordogne, France, 11th September 1992
Small, spineless tree in meadow, height 3-4 m. Summer shoots densely pubescent. Leaves elliptic-oblanceolate. Leaves of lateral spurs glossy, elliptic-oval, 6x3.5 cm. Fruits roundish, drooping. Taste sweet. Pedicels pubescent, length 6-10 mm, diameter 1.3-1.7 mm. *Insititia* features: size and taste of fruits, stones, habitus. *Spinosa* features: leaves. Identical type: Massalve, Dordogne.

CHAL-95-1: Chalaux, Morvan, France, 3rd September 1995
Very productive tree with abundant rootsuckers at the edge of the village, height 5 m. Summer shoots almost glabrous. Leaves oval or elliptic, 5.5x3.5 cm at maximum, on average 3x2 cm. Fruits ovate to round or oval, drooping, thick bloom. Taste acid. Pedicels glabrous, length 6-8 mm, diameter 1.0-1.4 mm. *Insititia* features: tree dimensions, fruits. *Spinosa* features: foliage, stones.

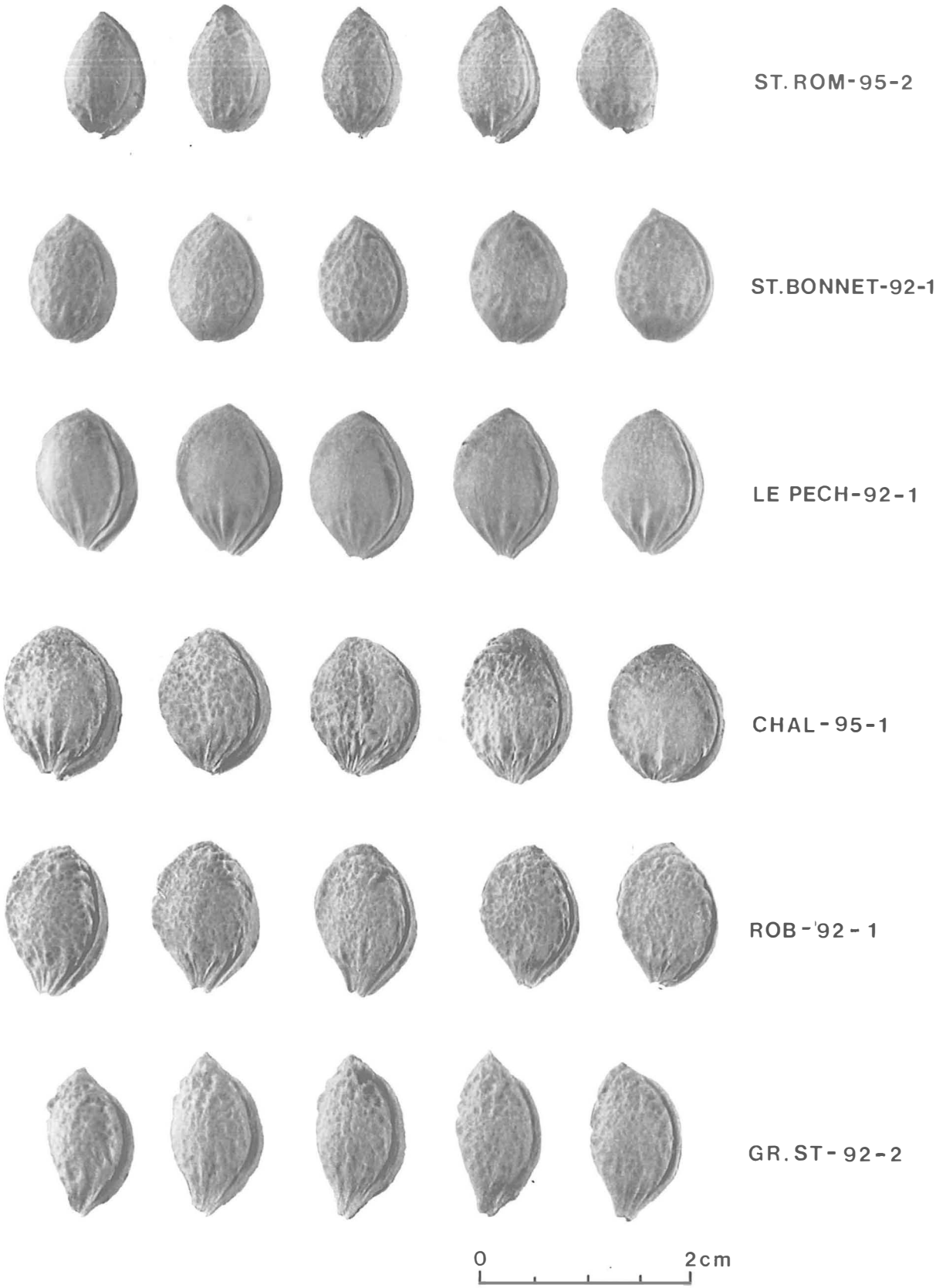
ROB-92-1: Robert, Dordogne, France, 1992
Thickets over c. 30 meter, height c. 3 m. Leaves oval, 3-4.5x2-3 cm. Fruits drooping, almost round, with or without bloom. Taste sweet. Pedicels pubescent, length 4-10 mm, diameter 1.0-1.7 mm. *Insititia* features: size and taste of fruits, stones. *Spinosa* features: leaves, growth properties. Germination rate c. 30%. Seedlings display heterogeneous growth.

GR.ST-92-2: Groningen 'Stadspark', the Netherlands, 26th August 1992
Sturdy tree with few spines, upright-spreading with few rootsuckers, height c. 4 m. Summer shoots pubescent. Leaves oval, 3.5-5x2.5-3.5 cm. Fruits drooping, slightly necked, oval, asymmetric, in outline resembling prunes. Taste acid. Pedicels pubescent, length 5-16 mm, diameter 1.2-1.5 mm. *Insititia* features: size and shape of fruits, stones. *Spinosa* features: leaves. Another specimen with similar stones grows in the park.

	ST.ROM-95-2	ST.BONNET-92-1
Fruits		
Number	15	11
Length	21.6(18.9-24.4)	23.0(21.7-25.4)
Thickness	17.6(15.2-21.1)	21.6(20.5-24.2)
Breadth	18.2(15.1-21.1)	22.6(21.6-25.3)
Stones		
Number	20	21
Length	11.5(10.3-13.0)	12.6(11.8-13.5)
Thickness	7.5(6.7-8.4)	8.9(8.1-9.7)
Breadth	5.4(4.8-6.1)	5.8(5.5-6.3)

	LE PECH-92-1	CHAL-95-1
Fruits		
Number	5	14
Length	26.4(25.4-27.0)	22.9(19.8-26.0)
Thickness	24.6(23.6-25.5)	21.4(18.2-24.7)
Breadth	25.9(25.1-26.8)	21.1(18.4-23.8)
Stones		
Number	18	20
Length	14.2(13.1-14.9)	13.6(11.2-15.5)
Thickness	10.1(9.3-10.7)	10.5(8.9-12.2)
Breadth	6.5(6.2-6.9)	7.2(6.2-9.0)

	ROB-92-1	GR.ST-92-2
Fruits		
Number	9	15
Length	21.7(20.4-23.4)	24.7(23.3-26.0)
Thickness	19.9(18.7-21.2)	19.3(17.9-20.6)
Breadth	20.6(19.4-22.0)	19.8(18.6-20.9)
Stones		
Number	21	25
Length	14.0(12.9-15.0)	15.2(13.3-16.5)
Thickness	9.8(8.9-10.5)	8.6(7.7-9.1)
Breadth	6.4(5.8-7.2)	5.6(5.1-6.5)


ST. ROM-95-2
ST.BONNET-92-1
LE PECH-92-1
CHAL-95-1
ROB-'92-1
GR.ST-92-2
0
2cm

AMPN-96-1: Ampney Saint Mary, Cotswold Hills, Gloucestershire, Great Britain, 9th September 1996
Productive shrubs bordering a path over ten metres, height up to 2.5 m. Summer shoots pubescent. Leaves obovate, smaller ones elliptic to oval, 3.5-6.5x2.5-5 cm. Fruits oval, drooping, sweet but not tasty. Pedicels smooth, also in pairs, length 7-13 mm, diameter 0.7-1.0 mm. Mostly *insititia* features with stones much resembling those of the local English damson. The fruits of this specimen are smaller than any of the collected English damsons. The combination of small (but full-grown!) shrubs and small damson-type stones suggests a crossing between damson and sloe. A type with similar stones was found at the edge of a small orchard in Sapperton, west of the town of Cirencester, Gloucestershire. This type has somewhat larger stones, necked and wry fruits and *spinosa*-type leaves.

PEI.'W-92-1: Peizerwold, province of Groningen, the Netherlands, 21st August 1992
Small-sized tree, alongside a sloe specimen in hedgerow between meadows, height 4 m. Summer shoots smooth. Leaves 6.5x3 cm. Fruits obovate, taste wry. Pedicels pubescent, length 7-11 mm, diameter 0.9-1.4 mm. *Insititia* features: habitus, leaves, drooping fruits, shape of stones. *Spinosa* features: taste of fruits, size of stones.

TU-90-15: Tuoro, locality Monticchio, Italy, 10th May 1990.
Stones from under tree with few rootsuckers in vineyard. Summer shoots thickly pubescent. Leaves crenate, oval to obovate, 7x4 cm. Leaves of lateral spurs variable, 2.5-6.5x1.5-4 cm. Leave margins serrate to crenate. Fruits oval, immature (therefore not measured). Pedicels thickly pubescent, length 15 mm.

	AMPN-96-1	PEI.'W-92-1
Fruits		
Number	19	15
Length	20.1(17.9-22.3)	18.3(17.1-19.7)
Thickness	17.1(15.6-18.7)	16.3(15.0-17.8)
Breadth	17.0(15.3-18.6)	16.9(15.4-18.9)
Stones		
Number	25	23
Length	13.6(12.2-15.5)	12.2(11.0-13.4)
Thickness	8.7(7.8-9.4)	7.8(7.1-8.4)
Breadth	6.4(5.8-7.6)	5.1(4.5-5.6)

	TU-90-15
Fruits	
Number	
Length	
Thickness	
Breadth	
Stones	
Number	20
Length	15.7(14.9-16.5)
Thickness	13.2(12.1-14.5)
Breadth	7.6(6.9-8.0)